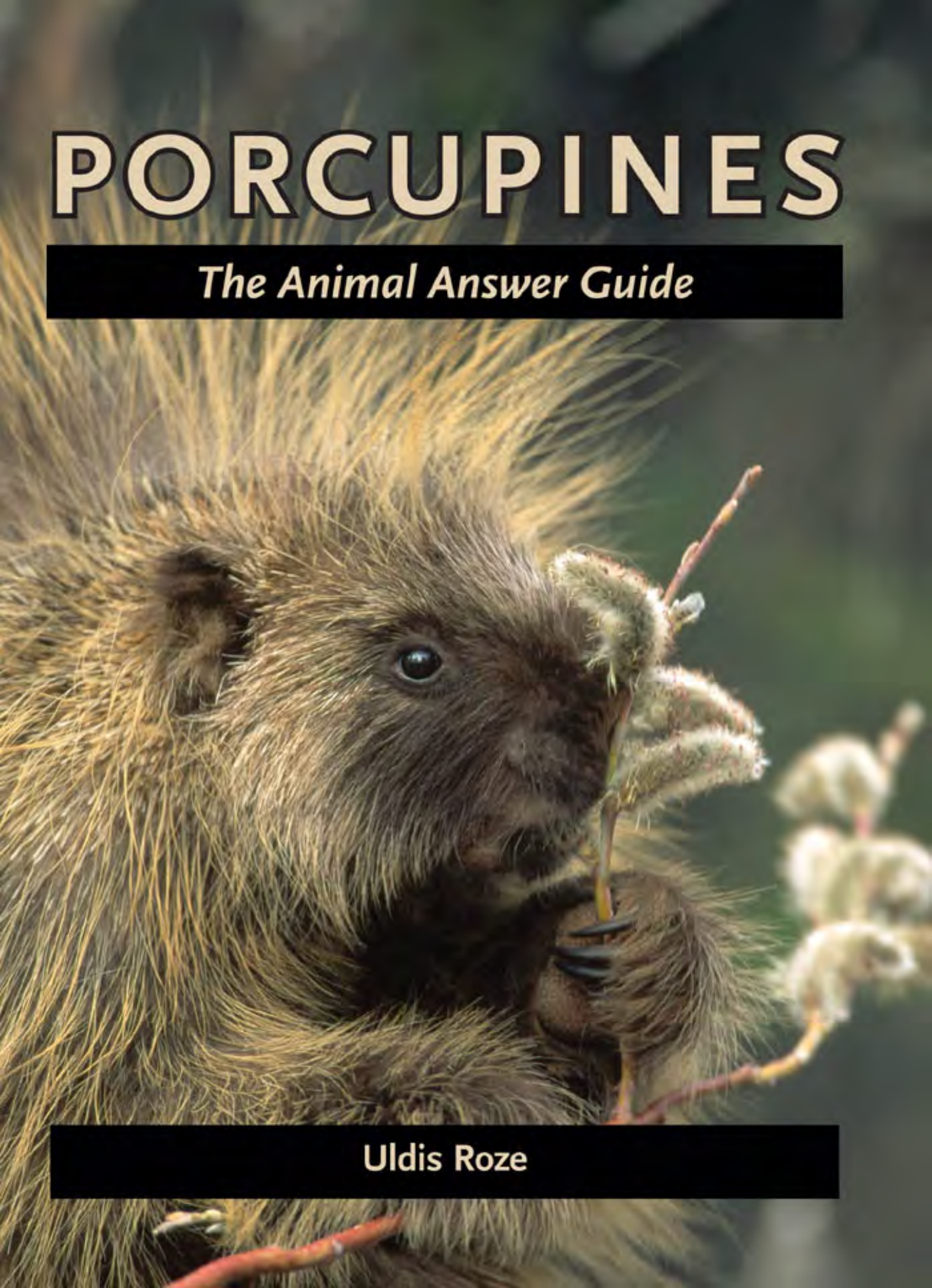
PORCUPINES
The Animal Answer Guide
Uldis Roze

VISIT…

Porcupines: *The Animal Answer Guide*

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Porcupines

The Animal Answer Guide

Uldis Roze

The Johns Hopkins University Press Baltimore

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"Friend porcupine," rumbled the hippo. "I am worn out struggling with you while you don't have a quill out of place. You are stronger than you look. Let us be friends!"

And forever after, the porcupine was happy to know that, despite his small size, the big animals respected him.

AFRICAN FOLK TALE

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These acts of generosity exemplify the traditions of the scientific community. In fact, it might be this tradition of cooperation that has been one of the driving forces of the worldwide scientific enterprise.

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Introduction

My involvement with porcupines started with a single species: the North American porcupine. I have spent nights sleeping under a porcupine high above in its forest feeding tree, have hiked through mountain forests tracking far-flung individuals, and have lived through both triumphs and tragedies of individual animals, such as the frenzied reaction of a human-raised orphan to her first scent of a porcupine in the wild or the long vigil of an old mother by the body of her son, who had fallen out of his brittle-branched feeding tree and been killed instantly. Such experiences make one appreciate the porcupines as long-lived animals with intricate personal histories.

In my first study, in 1984, I followed the tracks of individual porcupines in the snow. The snow tracks testified to an admirable economy of movement: optimal choice of feeding trees, awareness of other porcupines and potential predators, understanding of the terrain. In short, the porcupines showed a beautiful adaptation to their environment and food supply.

A similar fineness of adaptation to environment and lifestyle emerges in this comparison of the biological adaptations of porcupine species across the world, most of whom never experience snow and may never feed on tree bark. These cross-comparisons highlight the "creativity" of the evolutionary process. The 26 known porcupine species follow 26 different ways of life, a feat made possible by small and large physiological and anatomical innovations. Thus, we can describe at least two designs of the retina, six different designs of the tail, and at least seven different quill designs. All these are offshoots of an ancestral body plan that originated in the Old World Eocene, more than 40 million years ago. By looking at such differences, we can better appreciate the uniqueness of each porcupine species living today.

The question and answer format of the book allows the reader to start at any point as interests dictate. This requires each discussion to stand on its own feet, so certain facts are repeated across sections. But in each case, the information appears in a different context of a large and complex story. To sort out a stream of possibly unfamiliar species names, you may refer to a porcupine "who's who" in chapter 1.

In this book I have often felt like a speaker responding to questions from an erudite audience. Good questions can lead to insights that neither party anticipated—one definition of the scientific process. The questions can seem simple: What is a porcupine? What do porcupines eat? How do

they survive the winter? Or the questions may have layers of complexity: What are the porcupines' closest relatives? How do scientists tell porcupine species apart? How will global warming affect the porcupines? But one of the most important questions in this series is the last one: What don't we know about porcupines?

The amount we don't know about porcupines is staggering. This is partly because of the nocturnal, tropical-forest lifestyle of most porcupines of the world, but also because of the paucity of molecular biology studies of these animals and because their lifestyles have few parallels with other animal groups. These mysteries make porcupines a lure to scientists and nature lovers alike.

One of the great pleasures of working on this book has been the opportunity to explore these mysteries and discover aspects of porcupine life not known before. For instance, unlike all other New World porcupines, one South American species lacks one-way barbs on its defensive quills, leading to important differences in defense strategy (see chapter 2). Another discovery was the connection between the prehensile tails of New World porcupines and safety. Porcupines lacking prehensile tails were approximately 10 times more likely to fall out of a tree (see chapter 4).

Still another surprise was that in all porcupines with multicolored quills, the lighter-colored portions fluoresce under a black light. They do so because they carry brighteners, which make the porcupines more visible in the dark (see chapter 3). These observations were made with simple tools that are available to many readers. Yet each illuminates a broader aspect of porcupine biology.

In writing about 26 species of porcupine instead of just the North American species, two observations have jumped out. One is the many common threads of biology and lifestyle that link even the most distantly related porcupines of the world, such as the Old World and New World forms. All are long-lived, all invest heavily in their offspring, producing small numbers but offering long nurture to each. All are strict herbivores. All have developed sophisticated forms of a quill-based defense.

The other point driven home repeatedly is the lack of close studies of most of the porcupine species of the world, especially the Central and South American forms. It would be satisfying if this book helped stimulate more studies of these difficult but immensely rewarding animals.

Porcupines: *The Animal Answer Guide*

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Chapter 1

Introducing Porcupines

What is a porcupine?

Porcupines rank among the world's most widely recognized animals. Everyone knows these slow-moving, quilled creatures of fairy tales and movie cartoons. Despite porcupines' dangerous side, people who work with them will testify that they have sweet temperaments and sensitive facial expressions. What many people do not know is that porcupines are members of the mammalian order of Rodentia ("gnawers"), the largest order of mammals in the world, accounting for some 42% of the 5,400 species of mammals recognized today. As suggested by their name, the rodents are equipped for gnawing. Their front teeth (incisors) grow continually from deep in the jaw, and have a chisel-like cross section. Most rodents eat plant foods.

Porcupines do not make up a distinct taxonomic group of their own. They belong to two separate families of the Hystricomorph ("porcupine-like") suborder of rodents. One family, the Erethizontidae ("irritable family"), lives in the New World (North and South America). The other family, the Hystricidae ("porcupine family"), lives in the Old World (Eurasia and Africa). Porcupines are found on every continent except Australia and Antarctica.

Teeth. As part of their rodent heritage, the porcupines have 4 ever-growing incisors, 2 on top and 2 below. The open roots of these teeth extend deep into the upper and lower jaws. Unlike our own incisors, which grow to a certain size and then stop, the porcupine incisors elongate throughout life. They stay the same size because they are worn down continually by

the hard work of gnawing. The sharp, chisel-like contour is maintained by uneven wear: the hard enamel on the front of the teeth wears more slowly than the dentine in the back. These teeth are used for gnawing resistant materials like hard fruits, tree bark, and branches as well as more exotic targets like antlers and bones.

Behind the incisors lie 16 grinding ("cheek") teeth, 4 in each quadrant of the jaw. The cheek teeth are separated from the incisors by a space, the diastema. The diastema allows the animal to close its lips behind the incisors, thus keeping chewing debris out of the mouth. In most mammals outside the Rodent order, the space between the incisors and cheek teeth houses the canines—the stabbing and tearing teeth so prominent in carnivores. Porcupines have no canines.

The grinding, or cheek, teeth (4 premolars, 12 molars) work by a millstone-like action. Their grinding surfaces have alternating raised ridges formed by hard enamel and recessed valleys formed by softer dentine.

In all porcupines, the major chewing muscle, the masseteris medialis, passes through a skull opening (the infraorbital foramen) below the eye socket and attaches to the front of the lower jaw. This type of attachment is called hystricognathous ("chewing like a porcupine"). Hystricognathy strengthens the bite of the incisors as well as the grinding action of the cheek teeth.

Unlike the incisors, the porcupine cheek teeth have closed roots and do not grow after the grinding surfaces have been worn down. This sets the upper limit of a porcupine's life span, for when its teeth are worn away, it cannot feed itself. The premolars include a set of milk teeth that are replaced at the end of the second year of life. In very old porcupines, the premolars rise higher above the gum line than the molars.

Feet. Porcupines walk like miniature bears, on the naked soles of their feet. This mode of locomotion is called plantigrade. There are four toes on the front paws and five on the back. The toes of the New World porcupines are relatively long, making them useful in tree climbing. Likewise, the claws of New World porcupines are long and sharp. Old World porcupines are ground dwellers with relatively shorter toes, and the claws are worn short by digging and burrowing. Even the Old World long-tailed porcupine (*Trichys fasciculata*), which Nowak classifies as arboreal, has the short toes of its fellow ground-dwellers.

Tails. All porcupines have tails whose design is closely linked to the lifestyle of each porcupine species (see "How do porcupines use their tails," chapter 2). In South American porcupines (with one possible exception), the tails are prehensile—that is, they can be used to grasp tree branches and

act as a lifeline in a tree. The North American porcupine has a short tail that lacks prehensile function. Yet the tail remains essential for tree climbing by bracing the porcupine as it climbs or descends. In addition, this tail acts as a powerful quill delivery system. Because the tail is muscular and precisely controlled, it can move with lightning speed to drive quills deep into the body of a predator. In Old World porcupines of the genera *Hystrix* and *Atherurus*, the tail serves as a warning organ. Their tail tips carry highly specialized quills that can be vibrated to produce a rattlesnake-like warning sound. In the Old World long-tailed and brush-tailed porcupines, the tails are easily lost during a predator attack.

Quills. All porcupines carry quills, which are modified hairs deployed in the animal's defense. Individual quills are equipped with piloerector muscles that elevate or relax the quill as needed. A quill has a horny outer sheath and a spongy central medulla that thickens and stiffens it while remaining lightweight and air-filled. Quills of most New World porcupines have one-way barbs that make them difficult to remove once lodged in the flesh of a predator. The barbs act as ratchets that engage body muscles to pull the quill deeper into the body.

Quills are sophisticated structures that do much more than burrow into flesh. Specialized quills warn would-be predators with visual, auditory, or olfactory signals. In the North American porcupine, quills carry an antibiotic coating that minimizes the injury of self-quilling. The air spaces in quills serve as part of the body's heat shield and as flotation devices that help porcupines swim. Most porcupine quills have a detachment mechanism that comes into play following contact with the predator. Without this, the porcupine might find itself tied to the predator by its own quills. Quills are the original smart weapons, and I explore their properties further in chapter 2.

Although all porcupines carry quills, not all mammals with quills, spines, or bristles are porcupines. The porcupine look-alikes include such unrelated mammals as echidnas (order Monotrema—egg-laying mammals), hedgehogs (order Erinaceomorpha—"hedgehog-like forms"), and tenrecs (order Afrosoricidae—"African shrews"). Also excluded are the spiny mice, which are rodents of the mouse family, and spiny rats, which are New World Hystricomorph rodents that do not belong to the family Erethizontidae but make up their own family, the Echimyidae ("spiny murids").

How many kinds of porcupines are there?

Currently, 11 species of Old World porcupines are recognized. In describing these, I follow the taxonomy of Wilson and Reeder's *Mammal Spe-*

cies of the World (3rd ed.), a widely used reference. The New World has 15 species, for which I follow the taxonomy of Robert Voss, curator of mammals at the American Museum of Natural History and the world's leading authority on New World porcupines. Briefly, the porcupine genera are as follows. (See appendix A for a more detailed summary.)

Old World porcupines (family Hystricidae)
- *Trichys* ("hairy"): 1 species—long-tailed porcupine
- *Atherurus* ("grainy tail"): 2 species—brush-tailed porcupines
- *Hystrix* ("porcupine"): 8 species—crested porcupines and relatives

New World porcupines (family Erethizontidae)
- *Chaetomys* ("bristly mouse"): 1 species—thin-spined porcupine
- *Coendou* (Brazilian native name for porcupine): 13 species—prehensile-tailed porcupines
- *Erethizon* ("irritable"): 1 species—North American porcupine

The numbers of species recognized, however, are in flux. For example, 100 years ago mammalogists believed that two species of porcupines lived in North America, a black-and-white form in the east, *Erethizon dorsatum*, and a yellow-haired form in the west, *E. epixanthum*. Today, the two forms are considered members of the same species, differing only in minor ways and able to interbreed and produce fertile offspring. Conversely, the number of recognized South American porcupines has been increasing. Robert Voss of the American Museum of Natural History and Maria da Silva from the Amazonia Museum at Manaus described two new species in 2001, *Coendou ichillus* and *C. roosmalenorum*.

Among South American porcupines, the possibility exists that a number of currently recognized species may in fact be species complexes. Robert Timm and Roger Price have suggested that the bicolor-spined porcupine, *Coendou bicolor*, may be a species complex because porcupines at opposite ends of the species range carried different, closely related species of body lice. The Paraguay porcupine, *C. spinosus*, may represent another species complex, as suggested by Timm and Price, who noted an unusually large number of lice species (seven) on this species. Other New World porcupine species typically carry just one or two species of lice.

Suspicion has also fallen on the species integrity of the Brazilian porcupine, *Coendou prehensilis*. This large-bodied porcupine has an enormous species range, roughly comparable to that of the North American porcupine. In addition, the species shows great variation in quill coloration. Voss and daSilva note that the Brazilian porcupine may actually be a cluster of several closely related species. The suspicion has recently matured into certainty. In 2011, Yuri Leite and coworkers sequenced a mitochondrial gene of two *C. prehensilis* individuals from opposite ends of the species range.

The two individuals were shown to belong to different species. The new species has not yet been described (and does not appear in the list in appendix A).

Ultimate resolution of porcupine evolutionary relationships will probably have to be based on genetic evidence, and this will require more extensive DNA analysis than has been done. Until we fill this information vacuum, the species count of recognized porcupines will remain in flux.

Who's who among the Old World porcupines?

Of the 11 species of Old World porcupines recognized today, 8 species belong to the genus *Hystrix*. Members of the genus share a common body plan, as detailed below.

Hystrix porcupines. *Hystrix* porcupines are the largest of all porcupines, and are considerably larger than Old World *Trichys* and *Atherurus*, or New World *Coendou* described later in this chapter. *Hystrix* body weights are in the 10- to 53-pound (4.5–24 kg) range. They have short limbs, dull claws, and tails lacking stout bristles; hence, they cannot climb trees for food or escape. Despite their short limbs, they are fleet of foot. They may use their claws to dig deep burrows in the ground, where they retreat during daytime for safety.

The stout quills of their backs and sides offer significant protection against their major predators, the large cats. *Hystrix* quills lack the one-way barbs of New World porcupines, but their large size and sharp tips keep predators well away from the porcupine's body. The short tails of the porcupines carry modified quills called rattle quills that can be vibrated to generate a warning buzz. The rattle quills are hollow and goblet-shaped. During porcupine-predator interactions, the porcupines run rapidly sideways and backwards, trying to impale their enemies.

In all species that have been studied, *Hystrix* porcupines are monogamous and live in family groups consisting of a mated pair and their immature offspring. Females are on average heavier than males, and the sexes show no external differences.

Adults typically forage alone, but young porcupines are accompanied by a parent who protects them. As a result, the young have high survival rates. Gestation times are about half as long as in *Coendou* species (about 100 days versus 210 days), and typical litter size is one or two babies.

Hystrix porcupines typically dig for their foods, consuming roots, bulbs, and tubers. They also eat tree bark during the dry season, and raid farms for crops such as potatoes, corn, and melons.

They have the same adult tooth complement as New World porcupines:

4 incisors and 16 grinding teeth, for a total of 20. Like the New World porcupines, *Hystrix* possess a caecum, a fermenting chamber at the junction of small and large intestines that aids the digestion of plant foods.

The eight *Hystrix* species are described in the following sections. All follow the *Hystrix* body plan described above but differ in body weight, pelage, and geographical location.

Cape porcupine (*Hystrix africaeaustralis*). The preferred habitat of the Cape porcupines of southern Africa is moist forest, but they also survive well in scrubland and savanna habitats. Cape porcupines are the largest rodents in Africa. Free-ranging animals in Zimbabwe average 39 pounds (17.6 kg), with a maximum of 53 pounds (24 kg). Females are about 10% heavier than males. The porcupines carry an erectable crest of coarse white hairs from the top of the head to the top of the shoulders. Behind this lie large quills with alternating black and white bands. The erected crest and quills add to the apparent size of the porcupine during a threat display. The rattle quills, which also figure in the threat display, are unusually long in this species, typically more than 6 centimeters.

Crested porcupine (*Hystrix cristata*). Crested porcupines (*cristata* means "crested") are found in North Africa and in Europe. The European population is genetically related to the population in Tunisia and was probably introduced from North Africa. The date of introduction is uncertain.

Crested porcupines are closely related to Cape porcupines and Indian crested porcupines (*H. indica*). Like these sister species, crested porcupines have large body sizes. They have white, erectable crests of coarse hairs over the head, neck, and shoulders.

While all *Hystrix* species are nocturnal, the crested porcupines show less severe light avoidance than do the Indian crested porcupines to the east.

Indian crested porcupine (*Hystrix indica*). The southwest Asian species *H. indica* ranges furthest north of all the *Hystrix* species, extending into the Caspian and Aral region. Fifteen specimens from Israel weighed an average of 30 pounds (13.6 kg), with females 20% larger than males. Like Cape and crested porcupines, Indian crested porcupines have an erectable crest of coarse hairs. In Indian crested porcupines, the crest is black. The crests of *H. africaeaustralis* and *H. cristata* are white, a useful diagnostic criterion.

The porcupines are highly light-aversive, emerging from their dens only in total darkness. During winter months, even bright moonlight keeps the animals below ground.

Himalayan porcupine (*Hystrix brachyura*). Himalayan (sometimes called Malayan) porcupines are found in Southeast Asia and have weights of 22 to 40 pounds (10–18 kg). They are most closely related to Sunda porcupines, *H. javanica*, with which they are linked in the subgenus Acanthion. They lack the prominent crests of Cape, crested, and Indian crested porcupines, instead having a crest that is inconspicuous and easily overlooked. The large quills of the back are square at the base and rounded at the top. The species name, *brachyura*, refers to their short tails, which carry the typical rattle quills.

These porcupines occupy forests as well as adjacent open areas. They emerge at night to forage along well-trodden runways on tubers, tree bark, vegetation, and fallen fruit.

Sunda porcupine (*Hystrix javanica*). Sunda porcupines, from Java and Bali, lack crests and are most closely linked to Himalayan porcupines, *H. brachyura*, with which they are linked in the subgenus Acanthion. Though Sunda porcupines are primarily a lowland species, they have been found at altitudes up to 5,200 feet (1600 m). They are found most often in secondary and degraded habitats. The population is stable.

Thick-spined porcupine (*Hystrix crassispinis*). Thick-spined porcupines, a stable population found on Borneo, occupy a wide range of habitats, from native forest to cultivated areas. These porcupines are most closely related to Philippine (*H. pumila*) and Sumatran (*H. sumatrae*) porcupines, with whom they are linked in the subgenus Thecurus.

Philippine porcupine (*Hystrix pumila*). *Hystrix pumila* are found on the Philippine islands of Palawan and Busuanga, where they occupy both undisturbed and secondary forests and lowlands as well as mountainous areas. They also forage in scrubland and farmland. They can dig their own burrows or shelter in rock crevices or under tree buttresses. Small by *Hystrix* standards, their body weights range from 9 to 12 pounds (4–5.5 kg). The quills are flattened and grooved and are almost completely black, with only a small white base.

Philippine porcupines, linked with thick-spined porcupines (*H. crassispinis*) and Sumatran porcupines (*H. sumatrae*) in the subgenus Thecurus, are classified as vulnerable by the International Union for Conservation of Nature (IUCN). The population is declining because of deforestation and losses to hunting and the pet trade.

Sumatran porcupine (*Hystrix sumatrae*). Sumatran porcupines are linked in the subgenus Thecurus to Philippine porcupines and thick-spined por-

cupines. They lack erectable crests and have flattened, dark-colored quills up to 6 inches (16 cm) long, often white-tipped. Rattle quills develop at maturity. The porcupines look dark, with light splotches. Average body weights are 10.4 pounds (4.7 kg).

Sumatran porcupines dig burrows, which they line with plant material. They can also find living space in rock crevices or under fallen trees. The porcupines feed on wild fare like roots, tubers, and bark, but also raid cultivated crops such as sweet potatoes, banana, corn, melons, and mango. Though they are hunted for meat, their population is stable.

Other Old World porcupines. In addition to the eight *Hystrix* species, the Old World porcupine group includes two species of brush-tailed porcupines and the small long-tailed porcupine. The brush-tailed porcupines possess conspicuous tails that have a "brush."

African brush-tailed porcupine (*Atherurus africanus*). With an average weight of 7.5 pounds (3.5 kg), the brush-tailed porcupines from West, Central, and East Africa are somewhat smaller than North American porcupines. Brush-tailed porcupines get their name from a white "brush" sprouting from the tips of their tails. When alarmed, the animal can vibrate its brush to produce a sibilant warning sound. Tail tips are easily lost. When this happens, the remaining stump can sprout a new brush. Stout, barbless quills cover the back and sides of the porcupine.

The animals emerge after dark to forage on the ground. They subsist largely on fallen fruit but also dig for underground plant parts. African brush-tailed porcupines shelter in tree cavities, rock crevices, and burrows, which they do not dig themselves but may modify to suit. They live in "clans" of approximately three females and five to seven males each. The clans maintain exclusive territories.

Asiatic brush-tailed porcupine (*Atherurus macrourus*). Asiatic brush-tailed porcupines occupy dense forests of South and Southeast Asia. Physically they resemble the African species, with a broader base of the tail (*macrourus* = "large tail"). Their stout defensive quills on the back are flattened and grooved.

For shelter, the porcupines excavate burrows that can hold up to three adults. Their diets consist of roots, tubers, and green plants. One or sometimes two well-developed babies are born after a 100- to 110-day gestation, and females produce up to two litters a year. Young first leave the burrow after a week.

Long-tailed porcupine (*Trichys fasciculata*). The long-tailed porcupines of Southeast Asia are the smallest Old World porcupines, with adult body weights around 4.5 pounds (2 kg). They are considered the least-specialized members of this group, with a ratlike look, and short, grooved quills hidden among brown guard hairs and fur. During a threat display, they stamp their feet and erect their quills.

Their name comes from a relatively long, scaly tail that ends in a tuft of bristles. Unlike the tails of brush-tailed and crested porcupines, *Trichys* tails do not produce a sound when vibrated. The tails break easily at a point near the base. Without direct proof, biologists have speculated that the severed tail, with its white tuft, may distract a predator long enough for the porcupine to get away.

Long-tailed porcupines are forest dwellers and feed at night. Their broad diets include ground foods, primarily fallen fruit, as well as foods obtained by climbing trees and shrubs—leaves, fruits, bark, and occasional insects and small invertebrates.

Who's who among the New World porcupines?

Of the 15 species of New World porcupines recognized today, 13 belong to the genus *Coendou* and share a basic body plan. Details are given below.

Coendou porcupines. *Coendou* may be as small as 2 pounds (1 kg), with none larger than 11 pounds (5 kg). All have adaptations for tree climbing: sharp claws, relatively long digits, naked footpads capable of gripping branches, prehensile tails with friction pads, and stout bristles on the underside of the base of the tail. The small body weights may also be considered to be tree-climbing adaptations. The limbs are short, and *Coendou* move relatively slowly on the ground.

Coendou have 20 teeth: 4 rodent incisors and 16 grinding teeth. All have a digestive tract with a fermenting chamber, the caecum, which helps break down the complex macromolecules present in plant foods.

All *Coendou* carry sharp defensive quills with one-way barbs at the tip. Quills cover every part of the body except the face, the belly, inner limb surfaces, and parts of the tail. Fur is always present between the quills. It may be short and barely visible, as in the Brazilian porcupine, *C. prehensilis*, or long and covering the quills, as in the frosted dwarf porcupine, *C. pruinosus*, and many others.

Coendou have long gestation periods, on the order of 210 days (7 months). Porcupettes are born with eyes open, eight teeth erupted, and

quills tiny but ready to use. They receive long maternal care, ensuring a high survival rate.

Bicolored-spined porcupine (*Coendou bicolor*). The large South American porcupine *Coendou bicolor* occurs in the eastern Andean foothills and adjacent Amazonian lowland forest in Peru, Bolivia, and northwestern Argentina. Its quills are bicolored, with black tips, and are much longer along the neck, shoulders, and upper back than along the rump. This gives the animal a bicolored appearance, with a dark mantle and yellowish rump. There is no emergent fur. The porcupine has a relatively long prehensile tail and lives in trees. There is no information on its natural history or behavior.

Streaked dwarf porcupine (*Coendou ichillus*). The three adult specimens of streaked dwarf porcupines found in museum collections worldwide have all been collected from the densely forested Amazonian lowlands of eastern Ecuador and northeastern Peru. Field observations at La Selva Jungle Lodge in eastern Ecuador suggest that the species ranges further east in the territory north of the Amazon and west of the Rio Negro. The species was first described by Voss and da Silva in 2001. No ecological studies of the porcupine exist. The population status is unknown.

The streaked porcupine is a small species belonging to the "vestitus group" of porcupines, whose other members include *Coendou vestitus*, *C. pruinosus*, and *C. roosmalenorum*. Like other porcupines of the group, streaked porcupines carry both barbed bicolored defensive quills and thinner, longer, barbless bristle quills. In adult streaked porcupines, the underlying fur is short and does not cover the quills. The tricolored bristle quills, with whitish tips and bases and dark middle portions, produce a streaked effect in the back and sides. The rump, covered with dark-tipped defensive quills and lacking bristle quills, stands out as a dark contrast.

The porcupines have relatively long prehensile tails (85% of head + body length). A photo of a living streaked porcupine at La Selva Jungle Lodge shows the animal hanging head-down by its prehensile tail, feeding on bananas.

Bahia dwarf porcupine (*Coendou insidiosus*). Bahia dwarf porcupines, among the smallest known, are found in southeastern Brazil, where they inhabit the coastal Atlantic Forest but also venture into surrounding shrublands. Their short, bicolored quills are entirely covered by a pale fur. They share their species' eastern range with the thin-spined porcupine, *Chaetomys subspinosus*. A Bahia porcupine and a thin-spined porcupine may sit in the same tree without apparent discord. Nothing is known about the Bahia porcupine's life in the wild.

Black-tailed porcupine (*Coendou melanurus*). Black-tailed porcupines are medium-sized porcupines found in lowlands east of the Negro and north of the Amazon Rivers. They have bicolored quills that are entirely covered by long fur and a relatively long prehensile tail. Nothing is known about the species' life in the wild.

Mexican hairy porcupine (*Coendou mexicanus*). Mexican hairy porcupines are found in Central American forests from sea level to at least 7,700 feet (2350 m) but are more common at higher altitudes.

The backs and sides of the animals appear black or dark brown because a soft, emergent fur hides most of the yellow, black-tipped quills. The head is lighter in color because it lacks long fur and is covered in yellowish quills. The prehensile tail is 65% to 80% of the head + body length. The species is geographically variable: there are differences between montane and lowland specimens, and between Mexican and Panamanian specimens. DNA from the variant forms has not been sequenced to confirm that all are members of the same species.

Mexican porcupines are arboreal but will descend to the ground to cross roads and clearings. They feed primarily on ripe and unripe fruits and seeds, and on tree leaves when fruit is scarce. By day they den in hollow trees or sit on a tree branch among dense foliage, with the prehensile tail curled around a branch. Adult pairs have been found together in dens.

Black dwarf porcupine (*Coendou nycthemera*). The black dwarf porcupines of Brazil are found in lowland rainforests south of the Amazon river, from the River Madeira to the mouth of the Amazon. The porcupines lack emergent fur, and have bi- and tricolored quills. Their relatively long prehensile tails make them well-adapted for life in trees. Nothing is known of their life in the wild.

Brazilian porcupine (*Coendou prehensilis*). The large-bodied South American porcupines called Brazilian porcupines actually have an enormous species range extending beyond the borders of Brazil. They occur in most of South America east of the Andes, and south to northwestern Argentina and eastern Paraguay. Because of the large species range and the large natural variability of this porcupine, biologists have long wondered whether the Brazilian porcupine may be a complex of closely related species. Brazilian scientists working with Yuri Leite have recently confirmed this by DNA sequencing. Porcupines from the eastern and western ends of the species range differed as much as separate species do.

Brazilian porcupines have bi- and tricolored quills that in adults hide the short fur. The relatively long prehensile tail (100% of head + body

length) and enlarged footpads adapt the porcupines for life in middle and upper layers of the forest canopy, where they forage nocturnally on immature fruits.

Females bear a single young and nurse for 15 weeks. The female can mate a few days after giving birth; hence, a new pregnancy can start while the porcupette is still nursing, and births can occur at any time of the year.

Frosted dwarf porcupine (*Coendou pruinosus*). Frosted dwarf porcupines are tiny: one partly disarticulated skeleton at the American Museum of Natural History fits into a box normally used to store the skulls of larger porcupines. The defensive quills of frosted porcupines are barbed and bicolored. In addition, the animals carry barbless bristle quills, a trait they share with streaked dwarf porcupines (*C. ichillus*), brown dwarf porcupines (*C. vestitus*), and Roosmalen's porcupines (*C. roosmalenorum*). In frosted porcupines, a long, soft fur obscures the defensive quills. The fur is predominantly blackish but carries pale tips. The result is a frosted appearance—hence, the common name for the porcupines.

As in *C. vestitus*, the tails of frosted porcupines from the mountains are short in relation to head + body length (50%). Frosted porcupines from the lowlands have significantly longer tails (70% of head + body length). Whether this reflects a difference in tree use is unknown.

All museum specimens of frosted porcupines have been collected from humid-forest areas (lowland rainforest for lowland specimens, cloud forest for montane specimens). No specimens have been taken from unforested areas.

The only feeding record for a frosted porcupine comes from a specimen shot by Robert Voss in a lowland Venezuela site. Examination of the stomach contents revealed a brown paste, possibly derived from chewed bark. There were no insect or seed fragments or other identifiable food particles.

Rothschild's porcupine (*Coendou quichua*). The Rothschild's porcupines of Panama and northern Colombia range from sea level to 10,800 feet (3300 m). They are found in lowland evergreen forests, secondary forests, cultivated areas, and montane rainforests.

These medium-sized *Coendou* have a dramatically contrasting pelage, with white quill tips scattered against a black background. The white contrasts are generated by long tricolored quills with white tips and bases, and dark middle portions. The rest of the body quills are bicolored, with white bases and dark tips. The body fur is short and hidden beneath the quills.

Rothschild's porcupines are geographically variable. Tail length varies between 55 and 90% of body + head length, with shorter tails found among montane specimens. Montane specimens also have smaller feet, narrower

nasal apertures, and less surface speckling. Similar geographic variation is observed among Mexican porcupines and bicolor-spined porcupines.

Rothschild's porcupines are arboreal and feed on fruit and perhaps leaves. No field studies exist.

Roosmalen's dwarf porcupine (*Coendou roosmalenorum*). Roosmalen's porcupines—known only from three specimens collected from both banks of the Madeira River, a major tributary of the Amazon—are possibly the smallest known porcupines. One specimen weighed only 1.3 pounds (0.6 kg), but the animal may have been emaciated. The species was described by Voss and da Silva in 2001 on the basis of the three specimens, collected in 1996 by Marc Van Roosmalen, a Brazilian biologist. The species' range and population status are unknown.

These porcupines are part of the vestitus group of *Coendou* porcupines, whose other members include *C. ichillus*, *C. pruinosus*, and *C. vestitus*. In addition to the barbed defensive quills, they carry barbless bristle quills. In Roosmalen's porcupines, the defensive quills are bicolored, with yellowish bases and brown tips. The bristle quills are tricolored, with pale bases and tips, and dark middle portions. Most of the quills are hidden by thick emergent fur, pale gray-brown to dark brown in color. There is a relatively long prehensile tail (85% of head + body length).

What little is known about the animals' natural history comes from the history of one of the three collected specimens. The animal was captured when it emerged from a felled tree. Kept as a pet, it was released every night to roam in the surrounding forest. It returned at dawn to sleep through the day in a box under the owner's house. The animal was later moved to the city of Manaus, where it lived for several months, eating a variety of seeds and fruit. It died of unknown causes while apparently in good health.

Stump-tailed porcupine (*Coendou rufescens*). Stump-tailed porcupines live in the mountains of Colombia, Ecuador, and northern Peru. After a break of thousands of kilometers, they are found again in northern Bolivia. The porcupines are found in forests at altitudes of 2,600–11,500 feet (800–3500 m).

In a 2011 study Robert Voss has compared a single specimen from Bolivia with its conspecifics far to the north, separated by difficult mountain terrain. He finds the animals morphologically indistinguishable. Why is there no geographical variation between such distant populations? Voss speculates: "Perhaps it is not fanciful to think that the Inca, who transplanted whole human populations from one end of the Andes to the other, might also have transported captive stock of this strikingly beautiful rodent over equivalent distances."

Stump-tailed porcupines are named for their short tails. At 40% of head + body length, the tails are proportionately the shortest in the genus. Nevertheless, in some specimens a rudimentary friction pad is visible, suggesting some prehensile function.

The pelage is made up of bicolored and some tricolored quills, whose red-brown tips give the coat its color and reflect the *rufescens* of the species name. Nothing is known about the animal's feeding habits, reproduction, social system, population dynamics, or other ecological parameters.

Paraguay dwarf porcupine (*Coendou spinosus*). Paraguay dwarf porcupines occur in eastern Paraguay, northeastern Argentina, northern Uruguay, and southeastern Brazil, where they encounter the southern ranges of the thin-spined porcupine and the Bahia porcupine. The Paraguay porcupines are found in moist forests, including the Atlantic Forest of Brazil and adjacent forests of Paraguay, Argentina, and Uruguay. The animals are found at altitudes up to 3,000 feet (900 m). The Paraguay porcupine study of Passamani showed that the porcupine feeds on the young leaves of six tree species.

Porcupines now linked in the species *C. spinosus* had been previously separated into a northern species, *Sphiggurus villosus*, and a southern one, *S. spinosus*. There is some doubt about the species integrity of *C. spinosus*. Timm and Price found that the species harbors seven species of porcupine lice. For other species in the genus, the number of louse species hosted is one or two.

In addition, there is geographic variation across the relatively large species range. Animals from the northern part of species range typically have orange-tipped tricolor quills and orange-highlighted fur; quills from the southern part of the range typically have yellow-tipped tricolor quills and fur with pale yellow highlights on the back and pale gray on the belly.

Brown dwarf porcupine (*Coendou vestitus*). The small brown dwarf porcupines are known only from the Andean foothills of Colombia's eastern cordillera, where they were last collected in 1925. For the next 85 years, no new specimens were found, and the species was feared extinct. Very recently, a fresh specimen has been obtained from the same area.

These porcupines have two kinds of quills: barbed defensive quills that are bicolored (with white or yellow bases and dark tips), and longer, thinner, barbless bristle quills (likewise bicolored). The presence of bristle quills links *C. vestitus* with three other small porcupines*: C. pruinosus*, *C. roosmalenorum*, and *C. ichillus.* The quills are largely obscured by a soft, brownish fur that gives the brown dwarf porcupine its common name.

The prehensile tail of the brown dwarf porcupine is only 50% of head + body length. This is the second lowest tail-to-body ratio in the *Coendou*

Paraguayan dwarf porcupine, *Coendou spinosus*. The quills of this small porcupine of southeastern Brazil are almost entirely hidden by thick fur.
Photo by Eduardo Carvalho.

genus. Nothing is known about the animal's natural history or behavior, and as noted above, its population status is unknown.

Other New World porcupines. In addition to species in the *Coendou* genus, the New World porcupines include the related North American porcupine, *Erethizon dorsatum*, and the distantly related thin-spined porcupine, *Chaetomys subspinosus*, which belongs to a separate subfamily.

North American porcupine (*Erethizon dorsatum*). North American porcupines have the largest species range among New World porcupines and are the only porcupine species to range far beyond tropical and subtropical habitats. They occur in northeastern and western United States and range all across Canada and Alaska up to the tree line in the north.

North American porcupines are also the largest New World porcupines. Animals in New York and Massachusetts average 11 pounds (5 kg); animals in Alaska have peak weights in excess of 20.5 pounds (9.4 kg). Males are approximately 20% heavier than females.

The quills are bicolored, with white bases and black or brown tips in

eastern specimens. The dark to light proportions of quill bodies vary across the body, creating contrasting patterns of light and dark: a white chevron in the back and a white tuft on top of the head. During quill erection, quills of the rosette region of lower back disseminate a unique warning odor.

North American porcupines diverged from *Coendou* some 7.5 million years ago and are now assigned to their own genus, *Erethizon*, while remaining in the Erethizontinae subfamily. A major difference between *Erethizon* and *Coendou* is tail design. In *Erethizon*, the tail is only 25% of head + body length and lacks prehensile function. It functions instead as a quill delivery system and as a tree-climbing appendage. The latter function makes use of the stout bristles on the tail underside.

Another *Coendou-Erethizon* difference is a higher basal metabolism in the North American genus. This allows the young to grow fast enough during spring and summer to achieve a body weight sufficient to survive the winter. Nonwinter foods are leaves, fruit, and mast. Winters are typically spent in dens from which animals emerge nightly to feed. The winter diet of tree bark and evergreen needles is low in calories and high in plant defense compounds, causing all porcupines to lose weight during this time.

North American porcupines mate in the fall and give birth to a single young in the spring. Porcupettes are born with their eyes open, quills in place, eight teeth erupted, and limited mobility. They are totally dependent on mother's milk for the first two weeks, after which they start to climb and begin to take green foods. Nursing continues for four months, until the onset of the fall mating season. At this time, juvenile females disperse out of their mothers' territories and establish new territories of their own. Females typically do not breed until their second year. Males remain in their mothers' territories but also move freely across the home ranges of adjacent females and other males. They become sexually mature at age two but must battle older males for access to females.

Thin-spined porcupine (*Chaetomys subspinosus*). These small porcupines occur in the Atlantic Forest of southeastern Brazil and are strongly differentiated from other New World porcupines, having diverged from *Coendou* some 21 million years ago. In the family of New World porcupines, they occupy their own subfamily, the Chaetomyinae. Perhaps the most important difference between thin-spined porcupines and the rest of the New World porcupines is that the quills of the latter carry one-way barbs. The quills of thin-spined porcupines are barbless and stay with the porcupine after striking a predator. The quills are relatively short, slightly kinky, and brown for most of their length, with pale bases.

These porcupines are highly arboreal, seldom descending to the ground even when moving from tree to tree. They stay within their forest habitat,

not venturing into brush or open ground. Because the Atlantic Forest habitat of the porcupines is being destroyed, the porcupine population is declining, and the species is listed as vulnerable by the IUCN.

Thin-spined porcupines have relatively long prehensile tails, which are used as anchors while the animals are feeding or resting. Their diet is made up almost completely of tree leaves, making these porcupines perhaps the most folivorous species among all porcupines. The animals feed on a small number of pioneer tree species. Such tree species are abundant in the Atlantic Forest, allowing the porcupines to live on relatively small home ranges of 4.7 acres (2.14 ha). Activity begins only in total darkness. They share their species range with the Bahia dwarf porcupine, *Coendou insidiosus*, sometimes sitting in the same tree without visible conflict.

Why are porcupines important?

Porcupines are important intrinsically, as rare and distinctive wildlife whose sighting adds value to any walk in the forest. Beyond their value to hikers and nature lovers, porcupines are important because their activities have an impact on the environment around them. With the minor exception of tree voles, North American porcupines are the only arboreal folivores (feeders on tree leaves) on the continent, a niche filled in South and Central America by sloths, howler monkeys, and South American porcupines.

Brandee Diner and her colleagues have shown that North American porcupines are selective when feeding on quaking aspen trees. These researchers found that porcupines rejected trees whose leaves had high levels of two chemicals—the phenolic glycosides tremulacin and salicortin. Therefore, porcupines have the potential to affect the tree's evolution, with trees becoming genetically selected to possess these protective molecules. Because porcupines share their leaf-eating niche with insects (who show similar responses to tremulacin and salicortin), Diner cautions that the effects of aspen feeding by insects and porcupines must be separated to accurately measure porcupine effects on aspen evolution.

South American porcupines in the genus *Coendou* have more extreme arboreal adaptations than does the North American porcupine. A study of the Brazilian porcupine (*C. prehensilis*) by Charles-Dominique and coworkers in French Guyana found the animals consumed the immature fruits of eight tree species. Once a family of porcupines discovered a suitable tree, they foraged so efficiently that few if any seeds survived. The authors propose that as a countermeasure, the food trees of porcupines have evolved synchronous flowering and fruiting. Synchronous fruiting would provide so much food at harvest time that the porcupines simply could not eat it

all and some seeds would survive to grow into new trees. Tree species such as *Cecropia* and *Ficus*, which are not used by porcupines, flower asynchronously. The mammal species that feed on these fruits disperse the seeds rather than destroying them.

Old World porcupines perhaps have something to teach us about our effect on wildlife. Porcupines of the genera *Atherurus* (meaning "grainy tail," named for the beadlike quills of the tail) and *Hystrix* ("porcupine") are furtive, shy animals, unlike their New World counterparts. This may reflect coevolution with humans, who hunt them for food and rank them among the most prized game animals.

Several researchers have suggested a role for the Cape porcupine similar to that of elephants, who greatly affect their local environment. The continual digging of the Cape porcupine may create a substantial disturbance, one that keeps a savanna open and prevents its progression to closed woodland. Similar ecosystem influences have been described for the Indian crested porcupine.

Why should people care about porcupines?

Porcupines can bring intellectual adventure to their human cohabitants. When the great naturalist Alexander von Humboldt traveled the rivers and forests of present-day Venezuela and Amazonia over two centuries ago, he endured endless hardship and danger for the reward of visiting a new world. The tropical porcupines among which Humboldt traveled remain almost as little known today as they were in his time. And to a greater or lesser extent, that applies to all the other porcupines of the world.

Most porcupines are creatures of the wilderness, and to the careful observer, they can act as guides into their wilderness. Porcupines therefore represent adventure—the chance to travel where no human has traveled before.

What is the current classification of porcupines?

The order of rodents, to which porcupines belong, is subdivided into three major (and a number of minor) suborders: the squirrel-like rodents, the mouse-like rodents, and the porcupine-like rodents (the Hystricomorphs). Porcupines make up two families in the Hystricomorpha: the Hystricidae ("porcupines") of the Old World and the Erethizontidae ("irritables") of the New World.

In mid-twentieth century a debate simmered concerning the relationship between the Old World and New World families. Did the two share a common evolutionary ancestry? Or were the similarities between the two

The Brazilian porcupine, *Coendou prehensilis*, feeding in a tree branch. The porcupine holds onto the branch with its prehensile tail and enlarged hind footpads. Note the night-visible warning coloration of light head quills and white quill tips scattered along the body. Photo by Rodrigo Alvarenga.

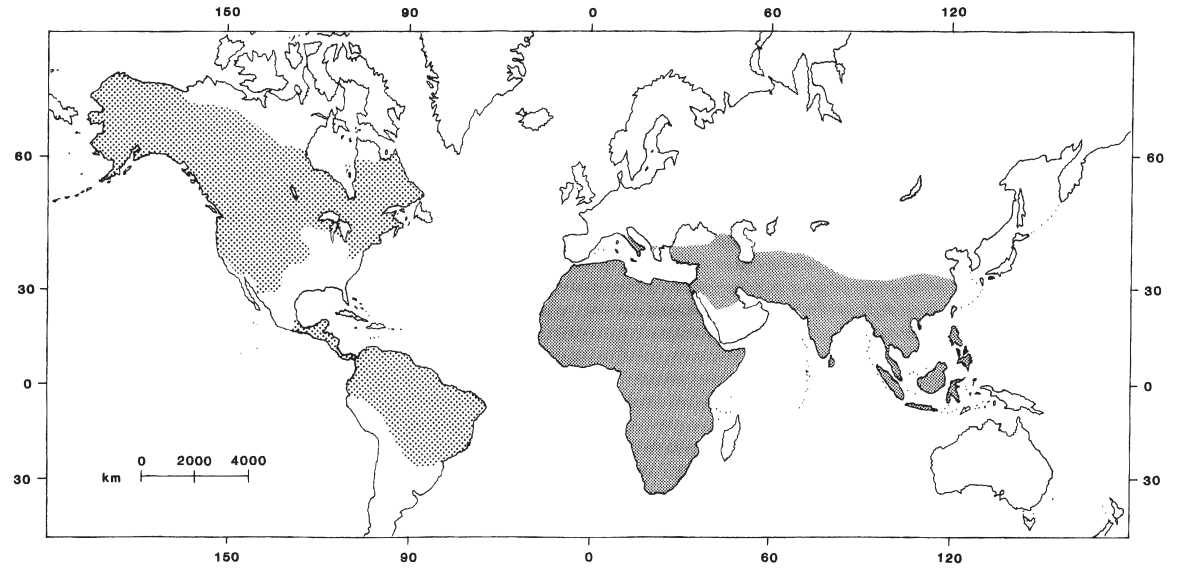
groups a matter of convergent evolution such as gives the dolphins and sharks a common body form even though they are not close relatives?

By 1985, the consensus had swung in favor of a common evolutionary origin for the two families, based on analysis of physical characteristics. By the beginning of the twenty-first century, this hypothesis had been confirmed by DNA evidence that suggested that all Hystricomorph rodents (not just the porcupines) have a common ancestry. This means that the two porcupine families have nonporcupine relatives. In the Old World, these relatives include a group of rodents called the Phiomorphs (cane rats, dassie rats, African mole rats). In the New World, the list of relatives is much larger and includes all of the Caviomorph rodents: guinea pigs, pacas, chinchillas, spiny rats, and others. Our best evidence suggests that all New World Hystricomorphs, including the New World porcupines, are descendants of Old World immigrants who arrived in a single colonization event some 38 to 50 million years ago.

What characterizes the major groups of porcupines?

Although Old and New World porcupines share important similarities of anatomy and reproductive modes, they have different ecological niches. Old World porcupines are highly nocturnal, move rapidly, and often possess diverse and highly specialized quills. Most live in family groups. They are ground dwellers that eat fallen fruit or dig for tubers and roots. Most Old World species cannot climb trees because they lack the proper anatomy and weigh too much: a 22- to 53-pound (10–24 kg) crested porcupine in a tree could not venture out on small branches.

In general, New World porcupines spend most of their foraging time in



Distribution of New World (open stippling) and Old World (closed stippling) porcupines. With the exception of the North American porcupine, *Erethizon dorsatum*, all porcupine species ranges fall in a band ranging in latitude from approximately 40° north to 30° south. The Mercator projection used in this map exaggerates the species range of *Erethizon*.

trees and possess adaptations to make this arboreal lifestyle possible. Many have prehensile (grasping) or appositional (woodpecker-like) tails, enlarged footpads with friction soles, relatively long fingers and curved claws for climbing tree trunks, and strong arm and leg muscles. They move slowly when on the ground. They feed on tree leaves, fruit, and tree bark.

When did porcupines evolve?

The most ancient porcupines in terms of evolution are the Old World forms, members of the family Hystricidae. Meredith and coworkers, using a combination of molecular and fossil dating, find that the Old World porcupines first appeared in the Eocene, 45 million years ago. There is some question about the evolutionary histories of the eight Asiatic members of the Old World group—the long-tailed porcupine, *Trichys fasciculata*; the Asiatic brush-tailed porcupine, *Atherurus macrourus*; and the six Asiatic crested porcupine species of genus *Hystrix*. None of these is known from the Asiatic fossil record prior to the Miocene (5 million to 23 million years ago). The assumption is that their ancestors arrived as overland migrants from Africa after a land bridge joined the two continents.

Meredith and coworkers date the arrival of Hystricomorphs in the New World from 39 million years ago, in the later Eocene. The New World

Hystricomorphs, called the Caviomorphs, rapidly diversified into the multiple descendant families we find in the Americas today. The New World porcupines form the oldest Caviomorph family. In their journey to the New World (presumably by "rafting" across the young Atlantic), the Caviomorphs preceded the primates (spider monkeys, howler monkeys, marmosets), who arrived about 17 million years ago.

One of the most recent arrivals on the porcupine stage is the North American porcupine. There were no porcupines in North America prior to the formation of the Panamanian land bridge some 3 million years ago. Thus, the North American porcupine or its precursor evolved in South America and migrated north once that land bridge was in place. Recent molecular dating by Vilela and coworkers of the split between the North American porcupine and the South American forms places the event in the late Miocene, some 7.5 million years ago. Rowe and coworkers give an earlier date of 15 million years ago. The fossil record of South American porcupines is poor, and its interpretation filled with controversy.

Why is the North American porcupine successful?

Among New World porcupines, the North American porcupine, *Erethizon dorsatum*, stands out by virtue of its exceptionally large species range. Only one other New World porcupine can match it—the Brazilian porcupine, *Coendou prehensilis*, whose species range is roughly equivalent in size. All other Erethizontids have ranges only one-tenth as large or less. The success of *Erethizon*, a South American immigrant, is all the more striking when considering how few other South American natives became permanently established north of Mexico when the Panamanian land bridge joined the two continents 3 million years ago. Only three other South American species have crossed to the north and remain there today: two species of armadillos (*Dasypus* spp.) and the opossum (*Didelphis virginiana*). None of them hold species ranges as extensive as *Erethizon*'s.

Another way to think of the success of *Erethizon* is to note how many South American mammal families have sent no permanent representatives beyond Central America:

No anteaters, suborder Vermilingua, 2 families (4 spp. in South America)
No sloths, suborder Folivora, 2 families (6 spp.)
No spiny rats, family Echimyidae (87 spp.)
No primates, 4 families (128 spp.)
No tapirs, family Tapiridae (3 spp.)
No agoutis, family Dasyproctidae (13 spp.)

No pacas, family Cuniculidae (2 spp)
No chinchillas or viscachas, family Chinchillidae (7 spp.)
No chinchilla rats, family Abrocomidae (10 spp.)
No tuco-tucos, family Ctenomyidae (60 spp)
No rock rats, degus, or viscacha rats, family Octodontidae (13 spp)
No guinea pigs, maras, capybara, family Caviidae (18 spp.)

This list excludes the bats. Of 248 South American bat species known today, a significant fraction range across North and South America, and for them the Panamanian land bridge was never a precondition for movement. Also excluded is the nutria (*Myocaster coypus*), now established in 16 states in the United States as well as in Europe, Asia, and Africa; members of this species escaped after being deliberately introduced into these areas for fur farming.

Then why did *Erethizon* succeed where so many others did not? We can only speculate, but we can begin by looking at the differences between *Erethizon dorsatum* and *Coendou prehensilis*.

Metabolic rate. *Erethizon* has a basal metabolic rate approximately twice that of *Coendou*. This allows it to use the short northern summer to speed juvenile growth, enabling the young to survive their first winter on their own. The growth spurt is just fast enough to allow for one litter per year. Northern forests, which renew themselves every spring, are well-suited to provide this food supply during most of the year. During winter months, when food supply is reduced, porcupines lose weight.

Heat conservation. The mixed pelage of *Erethizon*, consisting of quills, fur, and guard hairs, offers better heat conservation than the mostly quill pelage of adult *Coendou prehensilis*. While many of the dwarf porcupines of South America are heavily furred, their small body sizes are expensive to defend against cold because of high surface-to-volume ratios. *Erethizon* body weights, especially in northern populations, are substantially higher than those of any South American porcupines.

Tail structure. The tail of *Erethizon* is stubby and muscular, quilled on top and bristly below. The tail of *Coendou* is long and prehensile. The disadvantages of the *Erethizon* tail are readily apparent. Without a "fifth arm" to anchor themselves in the canopy, North American porcupines regularly fall out of trees. The evidence for this comes from skeletons in museum collections. An examination of 37 such specimens shows 13 with healed fractures: arm bones, leg bones, hips, shoulder blades. These represent nonlethal tree-fall injuries in the wild. Not all falls from trees are

survivable. Observations by Hale and Fuller, by Mabille and colleagues, and by myself document porcupine deaths following falls from trees. In *Coendou*, the picture is different. Of 31 museum skeletons I examined, only one showed a healed fracture.

But if the *Erethizon* tail is such a hazard to its owner, what countervailing advantages does it offer? First, better heat conservation. The long, naked-tip tail of *Coendou* invites frostbite in northern environments. It is for this reason that successful northern mammals have short extremities. Second, the short, muscular tail of *Erethizon* becomes a powerful launching platform for quills. When this porcupine confronts a predator, it is its tail that does most of the work of defense. The rapid tail flicks keep the predator farther away from the porcupine than simple erection of the back quills would. The force of the tail muscles can drive quills so hard they can disappear under the predator's skin.

Finally, and surprisingly, the belly-side bristles of the *Erethizon* tail make it a tree-climbing appendage. The tail bristles provide assistance for the heavy-bodied *Erethizon* in both climbing and descending trees. While *Coendou* species also use their tails for climbing support, their tails are less muscular and less strongly bristled.

In short, the *Erethizon* body plan outperforms *Coendou*'s in northern environments because of higher metabolic rate, improved heat conservation, and innovative tail structure. But improved body plan aside, one other factor has helped promote the northern fortunes of *Erethizon*: it faces no significant competitors in its niche of arboreal folivore. *Erethizon* alone can be lord of the northern forest canopies.

Chapter 2

Form and Function of Porcupines

What are the largest and smallest living porcupines?

The largest porcupines are the three Old World species of true crested porcupines (*Hystrix cristata*, *H. indica*, and *H. africaeaustralis*). Their weights range from 26 to 53 pounds (12–24 kg), and head and body lengths reach about 3 feet (93 cm). *Hystrix* are the largest rodents found on the African continent. Their large size and long, thick quills allow them to stand up to the most powerful of their natural predators—lions and leopards.

The smallest porcupines may be the *Coendou* species of the New World known as dwarf porcupines. Their weights range from 1 to 3 pounds (0.5–1.5 kg). The species include *Coendou roosmalenorum*, *C. ichillus*, *C. insidiosus*, *C. pruinosus*, and others.

It is no coincidence that crested porcupines are terrestrial, while dwarf porcupines are arboreal. A 50-pound porcupine in a tree would break branches.

Can porcupines see color?

The presence or absence of color vision is generally determined by an examination of the retina rather than by physiological or behavioral testing. Thus far, only the African brush-tailed porcupine, *Atherurus africanus*, has been studied for color vision.

All mammalian eyes have two kinds of photoreceptors (cells with pigments for trapping light): rods and cones. Rods have high light-trapping efficiencies and provide dim-light vision. Cones have lower trapping efficiencies but a more fine-grained synaptic processing, and are responsible for daylight

and color vision. For an organism to experience color vision, at least two kinds of cones must be present, sensitive to different wavelengths of light.

Humans and Old World primates have trichromatic color vision based on three cone types: red-, green-, and blue-sensitive. Most nonprimate mammals, including rodents, have dichromatic color vision, based on two cone types. The color world they experience is like that of a red-green color-blind human.

Peter Ahnelt of the Medical University of Vienna and his associates found only a single cone type, one sensitive to long-wavelength light, in the retina of the African brush-tailed porcupine. Although in theory, an animal with a single cone type might still see color through a cone-rod interaction, in reality such interactions are rare, and monochromatic vision shows the world in shades of gray.

The brush-tail's retina is densely packed with rods—approximately 400,000 per mm^2, among the highest densities observed in mammals. By contrast, its cone density is less than 1% of the rod density. Low cone densities are again a characteristic of nocturnal mammals. All these observations suggest the brush-tailed porcupine sees its world in dark and light, not color.

Only a few land mammals have been shown to have a single cone type; these include the raccoon (*Procyon lotor*) and the related kinkajou (*Potos flavus*). All of these are nocturnal animals. Their diurnal relative the coati (*Nasua nasua*) has two cone types and therefore has dichromatic color vision. In a nocturnal world, color vision works poorly because cones are present in low density in the retina and are inefficient in trapping light.

The brush-tailed porcupine is highly nocturnal, avoiding even the light of the moon. It forages along the forest floor, where light is dim. Its eyes possess a well-developed tapetum lucidum, a reflective layer behind the retina that sends light to the photoreceptors a second time. The tapetum is manifest as a bright white eyeshine at night, comparable to the eyeshine of a raccoon. Brush-tailed porcupines compensate for poor visual input with well-developed vibrissae, or whiskers, which give them tactile information about their surroundings.

Other Old World porcupines show equally strong specializations for life in the dark, including rich development of facial vibrissae. We might expect to find monochromatic vision among some or all of these, but no other Old World porcupines have been examined.

What can we expect among the New World porcupines? No species have yet been examined, but monochromatism in this group would be unexpected, for two reasons.

First, some New World porcupines are far less nocturnal than Old World forms. For a period every spring, the North American porcupine is

actually diurnal. And in a number of New World porcupines, the tapetum lucidum is poorly developed, as shown by the absence of strong eyeshine in *Erethizon dorsatum*, *Coendou prehensilis*, and other porcupines sampled by Voss and Emmons in their survey of South American rainforest mammals. The absence of strong adaptations to the dark among New World porcupines may be related to their being arboreal: they forage in treetops, where light is more abundant than it is on the forest floor.

Another reason to predict color vision among New World porcupines is because color vision is the norm among their close relatives. The retinas of three Caviomorph (New World Hystricomorph) rodents have been described: the guinea pig (*Cavia porcellus*), the degu (*Octodon degu*), and the cururo (*Spalacopus cyanus*). All have been found to be dichromatic, but dichromatic with a surprise. These animals are diurnal, though the cururo is fossorial (it burrows and forages underground). Their retinas contain some cones sensitive to short-wavelength light (S-cones) and others sensitive to long-wavelength light (L-cones). In most dichromatic mammals, the spectral sensitivities of the L-cones peak in the green to orange range, and in the S-cones in the blue to violet range.

In the guinea pig, the S-cones are maximally sensitive in the normal blue to violet region. But surprisingly, in the degu and the cururo, S-cone maxima fall in the near-ultraviolet (around 360 nm). These species thus can see in the ultraviolet. What biological function might the UV vision serve?

Other rodents (mostly nocturnal) have UV vision: the house mouse, the pocket gopher, the Siberian hamster, and the gerbil. Apart from rodents, no placental mammals with UV-sensitive S-cones have been discovered. Leo Peichl has hypothesized that UV vision might allow these animals to see the urine marks that rodents so often use, as urine is highly reflective in the UV. Thus, animals with UV vision could both see and smell their urine marks and also could gauge the age of the marks; fresh urine marks are brighter. This skill would surely be useful to the North American porcupine, which engages in frequent urine marking.

Extrapolating from related species, we can predict that New World porcupines will be shown to have a dichromatic color vision. And there is a chance that their color vision will have UV sensitivity. It will be interesting to see whether experimental findings match predictions.

Can porcupines swim?

Yes they can. All mammals can swim if forced to, though some, like house cats, avoid the experience. But North American porcupines enter the water readily in search of water lily leaves and stems, whose high sodium content satisfies their need for salt. The North American porcupine has

often been seen in the water, where it swims slowly but steadily. Among Old World porcupines, both crested porcupines and brush-tailed porcupines are known as good swimmers.

Though lacking the webbed feet or propulsive tail of a typical aquatic mammal, porcupines carry a built-in flotation device—their quills. A quill floats in water because its sealed interior is filled with a light, spongy matrix (the quill medulla). This property is exploited by fishermen, who may use large quills as fishing "bobbers"; the quills of the Old World crested porcupines are especially favored because of their large size and excellent flotation performance.

Evidence that the New World porcupine is at home in the water includes several reports of fish-porcupine encounters. A 1953 report by E. R. Kalmbach describes a rainbow trout caught on the Platte River in Colorado. The fish seemed healthy, but the process of cleaning revealed five small quills completely embedded in the tail muscle. All were oriented vertically in the body, and the tips of two of the quills had reached the skin of the back, near the dorsal fin. It seemed that the quills had entered on the belly side and worked their way upward. They had been in the flesh for some time, as the flesh surrounding some of the quill shafts was inflamed.

The author thought that a porcupine had been swimming in the river when its tuft of terminal hairs acted as a lure to trigger the rainbow trout attack. An upward flick of the porcupine's tail sent the fish away hungry. But the trout later forgot its lesson and struck the lure of the fisherman's fly.

Another fish-porcupine encounter was described in 2007 by Peter Cott and Neil Mochnacz in Canada's Northwest Territories. They angled a bull trout that had four porcupine quills in its upper lip. The fish was caught during spawning season, and the authors believe the trout attacked a porcupine that had intruded on its spawning grounds.

Can porcupines burrow?

Burrowing is restricted to the Old World porcupines, who often excavate their own spacious dens. For example, the Cape porcupine of South Africa, *Hystrix africaeaustralis*, may create a den 6 feet (2 m) below ground and several meters long. The den has a variable number of entrances; dens housing larger numbers of porcupines have more entrances. The den is occupied year-round though not all burrows are occupied. Christine Bragg and colleagues from the University of Cape Town counted burrows and porcupine densities in a geophyte-rich area of South Africa. (Geophytes are plants with underground storage organs and are eaten by porcupines.) She found 2.6 burrows per km^2, with a porcupine density of 8 animals per

km^2, higher than typical of semiarid environments but not as high as densities in moist forests.

Like the Cape porcupines, Indian crested porcupines (*Hystrix indica*) construct burrows. The burrows have long entrance tunnels, multiple exits, and a large central chamber. The excavated dirt is left at the entrance. The burrows of African crested porcupines (*H. cristata*) are so extensive that bats sometimes use them as roosts.

The burrows of Old World porcupines have special environments: the oxygen tension is low, and CO_2 concentrations are relatively high, leading to a rise in blood bicarbonate levels. Haim, Van Aarde, and Skinner have demonstrated that Cape porcupines, unable to excrete the CO_2 through their lungs, can expel it through their kidneys. Their urine is so bicarbonate-rich that it is alkaline.

Old World porcupines burrow not only to construct living quarters, but also to dig out their underground food sources. Bragg and colleagues found that in a semiarid region of South Africa, Cape porcupines moved 1.6 m^3 of soil per hectare per year, making up to 3,400 diggings per hectare per year. The disturbed sites encourage plant germination, so that porcupine diggings contain significantly more seedlings than adjacent areas.

By contrast, the North American porcupine cannot burrow, but it may use hollow trees and logs or natural rock crevices as underground dens for winter shelter or summer protection against predators and biting insects. The New World porcupines are arboreal; they climb trees for food and sleeping perches. Perhaps the sharp claws needed to climb would be dulled by burrowing. The claws of *Hystrix* are very short—too short to fit securely into crevices in tree bark.

What senses are best developed in porcupines?

The senses of all porcupines deemphasize sight, a daytime sense, and emphasize senses that work well at night: smell, hearing, and touch. This is because the porcupines are nocturnal: they move at night and sleep in the day. However, the nocturnal schedule is more strictly observed in some species than in others. For example, the Indian crested porcupine (*Hystrix indica*) is active only at night and is so photophobic (light-averse) that in winter months it ties its nightly emergence from its burrow to moon phase to avoid movements in bright moonlight. The African brush-tailed porcupine (*Atherurus africanus*) shows similar moonlight avoidance.

Phil Alkon and David Salz have suggested light avoidance as the reason that the range of the Indian crested porcupine species does not extend further north than the Caspian-Aral region (about 44° north). Above this latitude, summer nights become too short to allow sufficient foraging time.

The northern limit of the species range does not coincide with broad climatic or vegetation boundaries.

The North American porcupine, *Erethizon dorsatum*, is less photophobic. Though still primarily nocturnal, in early spring it may spend half its foraging time in bright daylight. It returns to a normal nocturnal schedule later in the spring and summer.

We naturally expect the sense of smell to be highly developed in Old World porcupines, which forage at night and on the ground—the very environment where smells are most richly presented. These porcupines are searching for underground roots and bulbs, and for fallen fruit in the forests. But the North American porcupine is also strongly dependent on its sense of smell. It navigates the forest at night to find distantly scattered feeding trees and rest trees. These it marks at the base with a few drops of urine.

I witnessed the sensitivity of a porcupine's nose in the fall of 2003, when I was rehabilitating a young porcupine whose mother had been hit by a car. Before its release in the wild, I was taking the porcupine on long walks in the woods to acquaint it with available feeding trees and den sites. On one of our walks, the baby porcupine found a linden tree in which a wild female porcupine had spent the night feeding. The female had left a urine mark under the tree. Even I, an effectively smell-blind *Homo sapiens*, could detect the urine by putting my nose close to the ground.

But the baby went into a frenzy. It furiously sniffed the ground again and again, vocalizing porcupine baby sounds and trying to climb the tree from which the porcupine urine had come. It was clearly responding to another porcupine.

We repeated our walk a week later. In the interim, a heavy rain had fallen, and high winds had combed the forest, which I assumed would erase olfactory messages like an eraser removes chalk on a blackboard. I let the little porcupine take the lead, and after a longish hike, we found ourselves under the previous week's linden tree. To my dull nose, not a whiff of last week's pungency remained on the ground, but the little animal spoke otherwise. It went through the same reactions, sniffing excitedly at the ground, vocalizing, and trying to climb. A beagle could not have given a more masterful performance.

The sense of smell is also highly developed in the Indian crested porcupine, *Hystrix indica*. Phil Alkon discovered this by tagging some of his animals with radio collars that sent back acoustic information about the animals' surroundings. The animals were often heard sniffing furiously during their nocturnal wanderings. These porcupines search for bulbs and tubers below the ground, and they find them by smell.

Hearing is another sense that shows high development in porcupines. I have had convincing demonstrations while radio-tracking tagged North

American porcupines in the winter. My animals were wearing radio collars with activity sensors. If an animal had not moved for several minutes, its radio signal would cycle into a slow mode. As soon as the animal moved its head, the beat would switch to a fast mode.

In the winter, most animals were sitting deep in their rock dens. They were dozing, as shown by the slow beat of their radio signals. I listened to the signal as I approached the den. The only sound I was making was the soft crunching of my snowshoes in the snow. But typically when I got within 30 feet (10 m) of the den entrance, the signal would cycle into the active mode. Deep in its den, the porcupine had heard me. It is unlikely that it was responding to ground vibrations. The rock core of the mountain lay under deep snow, and the rock floor of the den was cushioned by a thick layer of decomposed porcupine droppings.

Another nighttime sense is the sense of touch. In humans, the sense of touch is most highly developed in the fingertips: blind people read Braille by passing their fingertips over the tiny raised dots. Another human area with high touch sensitivity is the lips; all lovers know the sensitivity of the lips.

The sense of touch in porcupines is channeled through different receptors—their hairs and associated nerve receptors in the skin. In the North American porcupine, the touch-sensitive hairs are the guard hairs that emerge from the back and sides of the body and the vibrissae (whiskers) of the face and wrists. When a sleeping porcupine is touched lightly on a guard hair, it rouses immediately. Because the guard hairs and vibrissae are longer than the quills or body fur, the porcupine's zone of sensitivity extends outward well beyond its skin. This is especially useful in the tight confines of the tree canopy, where the animal must navigate nocturnally among tangled branches and leaves.

Presumably, a similar touch sensitivity exists among South American porcupines, who all forage at night in trees. They all have well-developed vibrissae. Vibrissae are especially well-developed in the Brazilian porcupine, *Coendou prehensilis*. In this species, the vibrissae reach out as far from the body as the animal could reach by maximally stretching its arms. To make a human comparison, we are talking about 2.5-foot whiskers.

But the whisker champions in the porcupine world are the Old World long-tailed porcupines, *Trichys fasciculata*, and the brush-tailed porcupines, genus *Atherurus*. In these species, the vibrissae extend well beyond the reach of the forearms. *Trichys* and *Atherurus* travel on the ground in night darkness; they may not emerge at all if the moonlight is too bright. Their vibrissae create a broad tunnel of contact in the dark. The vibrissae may be even more useful inside the dens (caves, burrows, hollow trees).

Porcupines' sense of sight is not entirely useless at night. However, night vision appears to be better developed in Old World porcupines than

Vibrissae (whiskers) of two Old World porcupine species. *Left*, In the long-tailed porcupine, *Trichys fasciculata* (museum specimen), the very long vibrissae provide tactile information about the surroundings while the animal moves in total darkness. *Right*, The Indian crested porcupine, *Hystrix indica*, has shorter vibrissae above the eyelids and around the muzzle for night foraging. American Museum of Natural History (*left*) and the Bronx Zoo (*right*).

in New World forms. Old World African brush-tailed porcupines and crested porcupines show a strong eyeshine when their eyes are illuminated at night. The eyeshine is due to a reflective layer behind the retina, the tapetum lucidum. In effect, the tapetum makes light travel twice through the retina, once as an incoming photon stream, then as a reflected one. Animals with tapetal eyes, such as whitetailed deer, have better night vision than those lacking the structure. Humans lack a tapetum and show no eyeshine. (The "red eye" seen in flash photos shows the blood vessels of the retina.)

Because the North American porcupine has only a weak eyeshine, its tapetal layer must be poorly developed. The same is true of its South American relative, the Brazilian porcupine. If these differences are confirmed in more species, it will be possible to generalize that Old World porcupines have better night vision than New World forms.

How do porcupines use their tails?

Tail function is one of the important ways in which porcupines of the world differ from each other. I have already mentioned the innovative tail of the North American porcupine, *Erethizon dorsatum*. *Erethizon's* tail is a weapons system: it drives quills with greater power and precision than would be possible with techniques such as head-butting, butt-bumping, or rolling into a ball. The tail of this species also forms part of the visual warning signal, creating a black-and-white contrast. It has good heat-conservation properties, allowing its owner to live far to the north of its evolutionary cousins. And very importantly, the tail of *Erethizon* functions as a tree-climbing appendage, anchoring the body as the animal makes its way

up or down a trunk. On the way down, the tail also serves a tactile function, exploring the surface of the tree trunk below. Without its tail, *Erethizon* cannot climb.

The tail of the Brazilian porcupine, *Coendou prehensilis*, serves an entirely different function: it grasps tree branches. In technical terms the tail is prehensile (from the Latin *prehendere*, "to grasp"). It shares this function with all New World porcupines of genera *Coendou* and *Chaetomys*. The tail of the Brazilian porcupine makes up about half its total body length: it is as long as the body and head combined. The hindmost third of the tail has a friction pad on its upper surface—an area of naked skin with a fingertip-like texture. When the friction pad comes into contact with a branch, the tail curls upward and wraps around the branch, anchoring its owner safely in place. Alternatively, the tail can spiral around the branch the animal is on. Porcupines with prehensile tails almost never fall out of trees.

Not only is the *Coendou* tail longer than *Erethizon*'s; it is also more flexible. It can accomplish its branch-gripping task because it carries more caudal (tail) vertebrae. A *Coendou* tail has 30 to 32 caudal vertebrae, while the typical *Erethizon* tail carries 15 vertebrae (with a range of 13 to 17). This big difference in caudal vertebral number makes it easy to distinguish *Coendou* and *Erethizon* fossils, providing the tails are preserved. Conversely, the reduced vertebral count in the *Erethizon* tail makes it stiffer, and hence more effective in quill delivery and in climbing support. Many South American monkeys also have prehensile tails, but for these animals, the friction pad is on the underside and the tail curls downward in grasping a branch.

The prehensile tail can also be used as a safety belt. Zortea and de Brito radio-tracked a thin-spined porcupine (*Chaetomys subspinosus*) in the Atlantic Forest of Brazil. The animal spent daytime hours sleeping in "roost" trees. During the majority of observations, the porcupine held onto its resting branch with its prehensile tail. Perhaps as a consequence, it chose to rest on branches that were thin, from 1 to 2 inches (2–5 cm) in diameter.

One South American porcupine has a tail that looks neither like the tails of its South American cousins nor like that of the North American porcupine. This is the stump-tailed porcupine, *Coendou rufescens*. The *rufescens* tail is not a stump like that seen on, for instance, most Dobermans. It looks stumplike only in comparison with the long tails of more typical *Coendou* species. A better name for the stump-tailed porcupine might be the shorter-tailed porcupine: its tail is only 40% of head + body length. One would expect a shortened tail to have poor prehensile function, yet some (not all) stump-tails have a rudimentary friction pad on their dorsal (upper) tail surfaces, not long enough to wrap around a branch but perhaps long enough to hook it like a coat-hanger.

Dorsal (back) view of tail of stump-tailed porcupine, *Coendou rufescens*. The tail is proportionately the shortest among South American porcupines. In some individuals, the upper tip of the tail is bare, forming a rudimentary friction pad. American Museum of Natural History.

The base of the stump-tailed porcupine's tail has quills on the upper surface, but the underside of the tail is bristled, like the tails of all American porcupines. The bristles would presumably be used in the same way, to assist in tree climbing. Thus, the stump-tailed porcupine's tail is a hybrid, combining features of both its North American and South American cousins. The animal cries out for field studies—all our speculation about its behavior is not backed up by observation in the wild.

The tails of Old World porcupines perform services still different from the ones mentioned so far. The brush-tailed porcupines (*Atherurus* spp.) have tails so distinctive that they lend their names to the porcupines. Brush-tailed porcupines are roughly the size of the North American porcupine and have thick, vicious quills that can pierce the toughest carnivore. The porcupines advertise their high defense capability by means of their tails.

Atherurus tails are long and tapering. A brushlike structure at the tip produces a loud, sibilant sound when vibrated. The sound is produced by hollow white quills (the platelet quills) that rattle against stiff bristles scattered among the platelet quills. It is the platelet quills of the tail that give the brush-tailed porcupines their genus name. *Atherurus* means "grainy tail." The grainlike effect is produced by the platelet quills, which are divided into alternating thin and thick segments. Brush-tailed porcupines can lose their tails during a predator's attack. When this happens, the porcupine grows a new "rattle" on the tip of the remaining stump.

In addition, the tip displays a visual signal. It is white and glows under UV illumination. This means it carries brighteners that make it more visible

during the dark-of-night foraging favored by the porcupine. The tail is held high when the animal is moving and thus functions as a warning organ, conveying its message both in the visual and auditory modes.

The tails of crested porcupines (genus *Hystrix*) are very short, but they also convey a warning signal. The signal is generated by tail-specific quills, the rattle quills. These quills begin development as normal quills, then lose their tips and morph into long-stemmed, hollow goblets. The short tail can vibrate at high frequency and produces an eerie buzzing sound generated by the rattle quills.

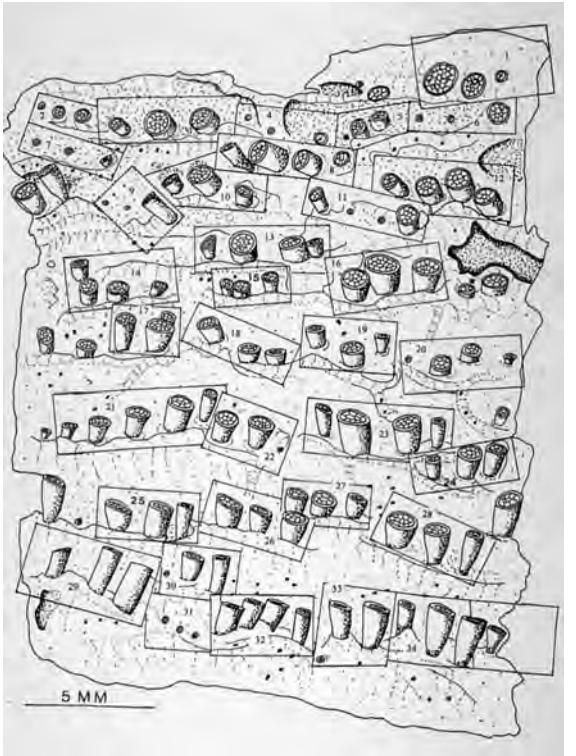
Among the most curious of tail functions is that of the long-tailed porcupine, *Trichys fasciculata*. As suggested by its name, the tail of *Trichys* is long for a porcupine. It is covered by scales for most of its length and ends in a tuft of bristles that does not produce a sound when shaken, as in the brush-tailed or crested porcupines. When the animal runs along the forest floor, it holds its white-tipped tail high like a flag. But about a third of the museum specimens of this porcupine are tailless.

Of the various theories offered to explain the high frequency of tail loss, the most plausible might be that the tail with its white tip is offered as a distraction to a predator during an attack. To date, the theory has not been experimentally confirmed. Unlike lizards, long-tailed porcupines cannot regenerate their tails once lost.

How many quills does a porcupine have?

For the North American porcupine, the number of quills is generally said to be around 30,000. The original source of this statistic is lost in the mists, which makes it difficult to evaluate. An early mention of 30,000 quills is found in a 1950 *National Geographic* article by Donald Spencer, but Spencer gives no indication that he made the measurement himself, nor does he suggest the methodology used. Presumably someone once took a square section of porcupine skin, counted the quills, and multiplied that by total quill-covered skin area. No one has either challenged or confirmed the measurement, but the number is now enshrined in the literature.

Why should one treat the 30,000 estimate with skepticism? Because quill densities vary considerably over the surface of the porcupine: they are high in the shoulder region and upper tail, low in the lower-back region. Not knowing how the measurement was carried out, we don't really know how many quills a porcupine has. Considering that a porcupine seldom uses more than 100 quills to ward off a predator attack, tens of thousands of spares would represent a considerable margin of safety.



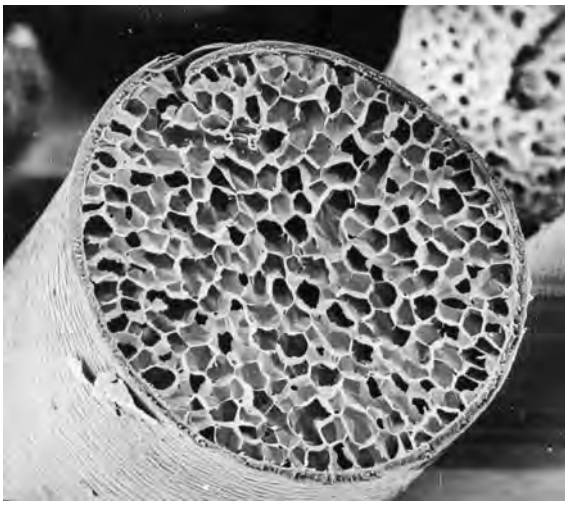
Surface view of the skin of the North American porcupine. Pictured is an 0.8 × 0.9 inch (2 × 2.3 cm) area from the thoracic (chest) region, containing 105 quills cut near the base. The quills are lined up in rows of 3 to 6. Examination of skin sections from different regions of the body can give an estimate of total quill count on the porcupine. Drawing by David M. Chapman. Reproduced with permission from Chapman and Roze (1997). © 1997 Canadian Science Publishers or its licensors.

Do quills provide good winter insulation?

The North American porcupine is the porcupine species most in need of winter insulation: its species range extends to the tree line in northern Canada and Alaska, and oftentimes beyond the tree line. During the long, severe winters, the animals do not hibernate but forage daily for their food.

The porcupines could not succeed in this task without the excellent insulation provided by their pelage. David Chapman and I have studied the pelage in histological detail. In our 1997 article we describe four hair types: quills, guard hairs, and two types of fur. Only the quills and guard hairs are piloerectible (able to form goosebumps). DeMatteo and Harlow point out that quills and guard hairs (long, rain-shedding hairs that project above the fur) can be controlled separately. As Chapman and I discovered, the fur is a passive element, lacking intrinsic piloerector muscles. In frigid temperatures, the porcupines press their quills against the body, while piloerecting the guard hairs. Bradley and Deavers estimate this compound pelage provides 67% more insulation efficiency than would a standard fur in an animal of its size.

The quills, guard hairs, and paraspinous hairs (long fur) are medullated: they contain cores of a spongy keratin (the protein of hair and nails).



Cross section of a quill from an adult North American porcupine. The quill has been sectioned in midshaft, where barbs no longer cover the outer surface. The surface is covered instead by scales of a type found in other hairs. The outer covering of the quill has a cardboard-like ultrastructure. The center (medulla) is filled with a keratinized foam. SEM photo by David M. Chapman.

Medullation adds to stiffness of the hair without significantly adding to its weight or replacement cost. Medullation also enhances the insulation value of the different hair types—think of the properties of polystyrene-foam coffee cups, likewise constructed of a foam-type core.

The fur, which accounts for much of the insulation value of the pelage, is shed in the spring in an annual molt. Thus, the porcupine changes its warm winter pelage for a cooler summer version once the winter is over. By fall, a fresh winter pelage is in place. The properties of the different hair types are summarized in the table.

There is one area of the North American porcupine's body that carries quills but is sparsely furred—the lower back, or rosette. With fur largely removed from the insulation mix, this region leaks body heat during cold weather: the rosette surface is about 6°C warmer than the upper back. The heat loss is unavoidable while the porcupine is moving. But when it retreats to its den, its loose skin allows it to tuck the rosette down towards its tail, effectively replacing it with the heat-conserving upper back.

Pelage of North American porcupine

Hair type	Pilo-erectability	Medullated	Annual molt	Insertion pattern	Length (mm)	Diameter (μm)
Quill	Yes	Yes	No	Rows of 3–5	25–100	700–1500
Guard hair	Yes	Yes	No	Single	to 160	250
Fur						
Paraspinous	No	Yes	Yes	Tufts of 5–8	11–17	100
Underfur	No	No	Yes	Single	3	50

Scanning electron microscope (SEM) view of the North American porcupine pelage. *Left*, Seven quills cut close to the skin, showing their spongy internal medullas, as well as a young quill that is emerging from the skin (*top right of photo*). Also pictured are two kinds of fur: the paraspinous hairs, which grow in clumps of 5 to 10 and contain an internal medulla, and the underfur. *Right*, The underfur, curly single hairs with solid cores. The shortest and finest hair type found in the porcupine, the hairs are about 3 mm long. The outside is covered with upward-pointing scales.
SEM photos by David M. Chapman.

Detailed studies of insulation efficiencies of the pelage have not been made in other species. Most of the species are tropical or subtropical in distribution, although many New World species live in the Andes mountains and experience a cool temperate, humid environment. The Old World Himalayan porcupine, *Hystrix brachyura*, has a species range that reaches into temperate habitat. It ranges from Thailand and Indonesia in the south to Nepal, Sikkim, and central China in the north. In 1969, two Himalayan porcupines escaped from a wildlife menagerie in Devon, England, and established a population in the wild that was able to reproduce and grow. While the winters of southern England are not severe, there is real cold and occasional snow. The pelage of this Old World porcupine was adequate to the task at hand.

In the warm interglacial of middle Pleistocene, a subspecies of the Himalayan porcupine ranged to latitudes further north than the British Isles: fossil remains of the porcupine have been described by Baryshnikov from the Ural Mountains of Russia, at latitude 59° north.

Does a porcupine throw its quills?

No porcupine can throw its quills. If such an ability ever evolved, it would do the quill-thrower no good for reasons of fundamental physics. The power residing in a moving object is given by its momentum—the product of the object's mass times its velocity. Because the mass of a porcupine quill is negligible, its momentum will likewise be negligible. It is for this reason that Native Americans tied stone arrowheads to their arrows, and medieval archers tipped their missiles with metal. Then why is quill-throwing such a persistent myth?

North American porcupines deliver their quills by a swipe of the tail. A porcupine's tail is thickly muscled and moves so quickly the eye can scarcely follow. In this case, the moving object is not the tiny quill alone, but the quill attached to a massive tail. Suddenly, the quills embed themselves in the predator, and a myth is born.

But the myth of porcupine quill-throwing preceded the discovery of America and the New World porcupine. The crested porcupine—which served as the heraldic emblem of the House of Orleans and, briefly, as the royal seal of France—was often pictured as launching a blizzard of quills against its enemies. This may have represented wishful thinking on the part of the French: one wants one's heraldic animal to project power. And since the porcupine was absent in France, who could challenge the myth?

What happens when a quill strikes a predator?

When a North American porcupine and its predator interact, things happen to both animals. In the porcupine, the collision of the quill tip with the predator drives the quill shaft back into the porcupine skin. A safety structure, consisting of a hard collagen ring encircling the quill shaft, prevents the quill from traveling deep into the body of the porcupine. However, the backward motion shears some of the attachment tissue of the quill base to the skin, making it easy to detach the quill from the porcupine body.

At the other end of the quill, the tip has penetrated the skin of the predator. The quill tip becomes anchored there by one-way barbs which resist backward motion and ensure attachment to the predator. Thus, as the predator separates from the porcupine, it carries with it a little forest of quills, wrong side out.

If the quill is small and has been driven deeply into the predator, it may continue its inward journey until it disappears beneath the skin. It now becomes a small internal projectile, propelled not by its momentum but pulled by the ratcheting of its one-way barbs against surrounding muscles.

Quill tip of Bahia porcupine, *Coendou insidiosus*. Like the quills of most other New World porcupines, it carries one-way barbs that anchor the quill in the body of the predator. SEM photo by David M. Chapman.

The ultimate fate of the quill varies. It may come to a halt against a bony surface such as a jawbone and become permanently encapsulated. It may travel to the skin, pierce it from the inside, and emerge, often far from the point of entry. Or it may pierce a vital organ and cause grave injury or death. Examples of serious injuries given by veterinarian M. D. Johnson and colleagues include piercing of the intestinal wall and setting up a fatal peritonitis (human examples); piercing of the eyeball, leading to retinal detachment and blindness (dogs); or piercing of the lower brainstem, causing circling movement (coyote). Quills may also end up in joints, causing lameness (dogs).

But quills don't have to travel far to do their work. A mouth filled with hundreds of quills is a common outcome following a predator attack. If untreated, the animal dies from starvation.

The quills of Old World porcupines lack one-way barbs and depend on physical impact to stab the predator. For successful penetration, the quills are longer and thicker than those of New World porcupines of comparable body size. And to cut more easily through the skin, the tips of Old World quills are typically not round in cross section, but lance-shaped.

One New World porcupine, the thin-spined porcupine of southeast Brazil, resembles its Old World relatives in carrying quills without one-way barbs. As noted by Gaston Gine (pers. comm.), these quills are not transferred to the predator following contact but stay with the porcupine. The quills, although lightly kinked, are sharp and stiff and cover the head, neck, and sides of the animal.

How does a porcupine minimize self-quilling?

In the North American porcupine, self-quilling is an unavoidable part of life in the trees. Self-quilling occurs when a feeding branch in a tree

snaps and the animal lunges for another branch for support. Self-quilling may also occur during predator encounters or when two males fight for dominance. In all cases, panicked thrashing movements may leave the animal pierced by its own quills. But while self-quilling may not be preventable, porcupines have evolved mechanisms to minimize the consequences.

First, unlike dogs, raccoons, and other mammals, North American porcupines are skilled at removing quills from their own bodies. They do this by pulling them out with their teeth. Kinked and flattened quills may be found under a porcupine's resting spot after it has groomed itself following a battle. Where teeth don't reach, porcupines can extract quills by levering them between the sides of their footpads.

A second line of defense against self-quilling is chemical: the quills of the North American porcupine are covered with an antibiotic that reduces bacterial infection. As I and my colleagues David Locke and Nick Vatakis discovered, the antibiotic is topical and consists of a mixture of free fatty acids, which kill Gram-positive microorganisms (bacteria that stain blue with Gram stain and possess simple cell walls). Two among many such Gram-positives in the porcupine's environment include *Clostridium perfringens*, the causative agent of gas gangrene, and *C. tetani*, the causative agent of tetanus. Specific protection against these organisms alone significantly reduces the dangers of a deep quill wound. Of course, the protection extends to the porcupine's predators as well. The quill is therefore a physical, not a biological, weapon in the porcupine's arsenal. It remains a potent weapon nonetheless.

Unlike the North American porcupine, the hedgehog has spines that are anchored in the skin by a bulbous base and thus locked in place. They can neither be transferred to a predator nor pushed backwards into the hedgehog. The hedgehog is therefore protected from self-quilling. But unlike the porcupine's "clean" quills, those of the hedgehog are "dirty." Hedgehogs engage in the curious behavior of self-anointing: they reach back with their long tongues and apply a frothy saliva to the spines. They often do this after ingesting a noxious food item such as a toad skin. Edmund Brodie reports that skin puncture by dirty spines causes significantly more pain than punctures by clean spines. The hedgehog can afford to make its spines dirty since it won't be suffering the consequences of self-quilling.

How long does it take to replace a lost quill?

For the North American porcupine, the length of time required to replace lost quills was investigated by Donald Po-Chedley and Albert Shadle at the University of Buffalo. They removed several thousand quills from

the tails and lower backs of six porcupines and marked the denuded patches with India ink. They then measured the time needed for regrowth. The quills replaced most quickly were the short quills from the top side of the tail, which were totally replaced in approximately 2 months. The longest quills of the back grew back in 3.5 months, but the medium-sized quills, such as those on the sides of the tail, took up to 9 months to replace.

Quill replacement took place in three stages. First, the replacement quill grew below the skin surface. This took up roughly half of the time of regeneration. Then the quill tip broke through the skin surface, and the quill grew to its full length. At this time, the quill had not yet reached its mature form, instead carrying a whiplike extension at the tip. When the whip was finally lost, the quill was ready for use.

Quill replacement times are diet-dependent. Po-Chedley and Shadle studied quill replacement in captive, well-fed porcupines. In 2011 Jessica Coltrane studied both captive and free-ranging porcupines in Alaska. The captives were kept on diets that lacked the plant defense compounds such as terpenes and tannins encountered by free-ranging porcupines. The diets of captive and free-ranging porcupines were otherwise similar. In the winter, captive porcupines maintained constant body weight, while free-ranging porcupines lost weight. The latter did not replace lost quills in the winter, while captive porcupines did.

Given the long periods needed for quill regeneration, and the suppression of that process during the winter, it might seem that a porcupine's denuded areas could be vulnerable following a predator attack. Several factors work to prevent or minimize this possibility.

First, a porcupine's quills, unlike the spines of a hedgehog or a tenrec, come in a range of sizes. If the longest outermost quills are lost, shorter ones below them will continue the defense. Second, the quills of a fully aroused porcupine point in different directions. Some point up, but others will point forward, backward, to the right, or to the left. A direct predator strike in any area will therefore leave some quills in place, ready for future use.

Porcupines are exempt from one disappointment of human males—they don't go bald with advanced age!

How did porcupine quills evolve?

It is not clear whether quills evolved once, in the Old World porcupines, and then were exported to the New World on the backs of ocean-crossing, quill-bearing Hystricognaths, or evolved independently in the New World because the ocean-crossing Hystricognaths were not porcupines. There are important differences between quills of Old World and New World

porcupines. Most strikingly, only the quills of most New World porcupines are barbed.

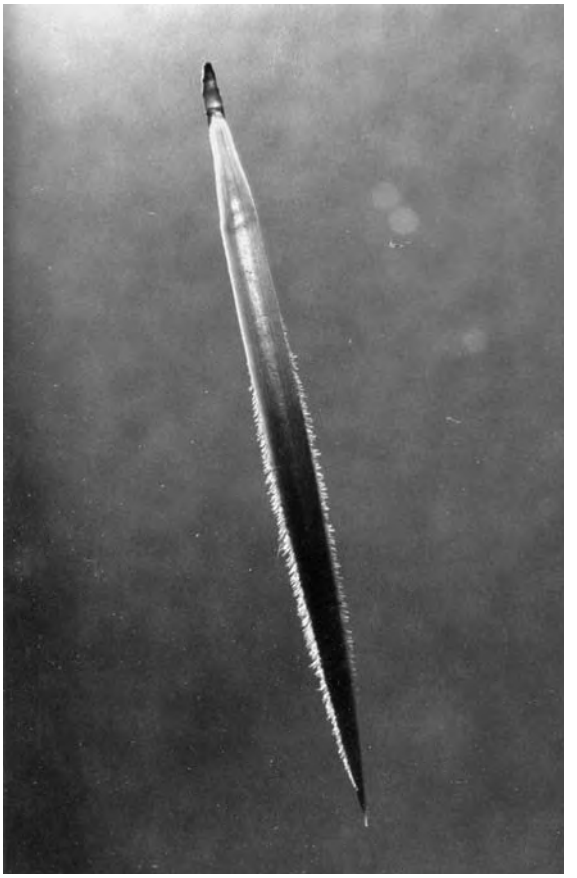
Another difference is the greater diversity of quill types in the Old World porcupines. They have rattle, platelet, or barbulated quills; quills with cross sections that are triangular, square, rounded, or flattened; and quills of astonishing size. By comparison, the quills of New World porcupines differ primarily in coloration and in the extent of the barbed surface. There are no Old World–New World differences in patterns of quill insertion.

Porcupine quills are modified guard hairs—the long, thick hairs that project above the fur of mammals to shed rain and snow and convey tactile information. To convert a guard hair into a quill, a number of features have to be added. The guard hair has to become thicker, to give it the ability to pierce the skin without buckling. The piloerector muscles (muscles that raise or lower the hairs) must be modified and enhanced to allow the hair/quill to be deployed instantly during confrontations and relaxed while at rest. In most New World porcupines, the guard hair must acquire barbs at the tip to make it more effective in skin penetration. And finally, the guard hair must develop a mechanism for separation from the porcupine following a quill strike. Otherwise, the porcupine may become tied to its adversary by means of its own quills.

Thus, the evolutionary transformation of a guard hair into a quill is a complex and extended affair. While the precise sequence of modifications is unknown, there are two other hair types that incorporate some of the modifications listed above. The first is the osmetrichium—a hair type that evolved to disperse odors. Osmetrichia tend to be thicker than regular hairs; they can usually be erected or relaxed at will; and they have an increased surface area that allows them to hold and disseminate the odorant.

An example of nonporcupine osmetrichia are the tarsal gland hairs of black-tailed deer (*Odocoileus hemionus*), as described by Müller-Schwarze and coworkers. The tarsal glands, present on the inside of the hock (heel) in both sexes, play a major role in social interactions in this species. The glands are activated by erection of a central tuft of osmetrichia holding a volatile mix of odorants. Dissemination of the odorants is facilitated both by erection of the osmetrichia and by the very high surface temperature of the tarsal glands.

The increased surface area of an osmetrichium is most easily generated by increased hair-scale separation, and hair-scales are the forerunners of quill barbs. Thus, a hair functioning as an osmetrichium may have served as a proto-quill to which the other quill-specific features were added. This proposal is pure speculation, but the speculation is supported by the fact that rosette (lower-back) quills of the North American porcupine serve an

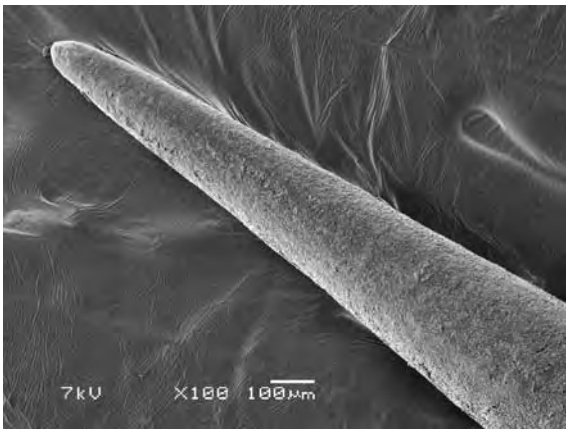


Barbulated quill from the back of an African brush-tailed porcupine, *Atherurus africanus*. The fuzzy extensions on the sides of the quill resemble the barbules of bird feathers. It is possible that the quill serves an osmetrichial (odor-disseminating) function.

osmetrichial function in addition to their general quill function: they disseminate a porcupine warning odor.

The osmetrichium-to-quill hypothesis would be most applicable to the New World porcupines, whose quill tips typically carry barbs. The quills of Old World porcupines are smooth. Yet even here, the hypothesis has some support, because the African brush-tailed porcupine, *Atherurus africanus*, carries a barbulated quill whose function is most easily explained as being osmetrichial.

A second candidate as a precursor for the quill is the vibrissa. Vibrissae are the long sensory whiskers on the faces of porcupines. Vibrissae, like osmetrichia, are stiff and in many cases movable. Lacking increased surface area, they are more difficult to convert into barbed quills. But the thin-spined porcupine, *Chaetomys subspinosus*, lacks barbed quills. It has a body covered with bristles and a head, sides, and upper back with sharp, stiff quills. Did quills evolve more than once in New World porcupines? To begin to answer such a question, one might ask whether there are differences in the follicle structures of *Chaetomys* as opposed to *Coendou* and



Quill tip of thin-spined porcupine, *Chaetomys subspinosus*, the only New World porcupine species with quills that lack one-way barbs. SEM photo by David M. Chapman.

relatives. Are there differences in quill-erection mechanisms? In developmental pathways of the quills? We don't know.

Why are a porcupine's front teeth orange?

When a baby porcupine is born, its incisors (front teeth) are white, not orange. The orange color develops in a matter of weeks, and it consists of iron salts deposited in the front layer of the enamel. According to the standard explanation, iron-coated enamel is harder than the unstained variety. The result is that the backs of the incisors, which are made of dentine and remain white, wear down more rapidly than the enameled front surfaces. The incisors are ever-growing and with use acquire a sharp, chisel-like contour, making them useful in such porcupine tasks as cutting branches, scraping bark and gnawing plywood.

Orange incisors are present in many rodents: beavers, squirrels, woodchucks, mice. They are absent in herbivores outside the rodent order: horses, cattle, sheep, antelopes. But there is a biological rule that states that all biological rules have exceptions. A number of rodent species have incisors as white as the rest of the teeth (cavies, naked mole rats). All rodent incisors are ever-growing and, even if white, acquire a chisel-like contour with use; the contour develops as a result of the normal difference in hardness between enamel in front and dentine in the back of the tooth. This is the same process that develops the ridges and valleys on the grinding surface of the cheek teeth.

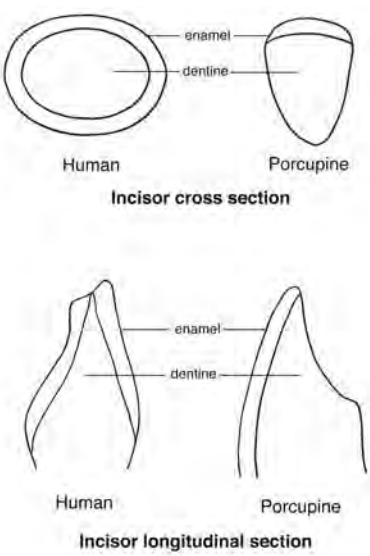
Then why the iron teeth of porcupines, beavers, and the majority of other rodents? Wighart von Koenigswald of Bonn University, who has spent a lifetime studying the enamel structure of vertebrate teeth, observes that the old theory of iron's role in rodent incisor function has never been proved. In rodent enamel, the iron pigment is localized only in the out-

ermost layer, which is too thin to determine the mechanical properties of the tooth. And the fact that guinea pigs can gnaw as well as other rodents should make us focus on the fundamentals of tooth structure.

All teeth contain at least two kinds of tissue: a hard, mineralized enamel and a softer, collagen-infiltrated dentine. In human teeth, the enamel forms a sheath around the dentine, and an incisor in cross section looks like a tree with a single growth ring. (Lower on the tooth is a third tissue type—the pulp.) In porcupine incisors, enamel covers only the front side of the tooth. Because of the difference in hardness, the dentine on the back wears away faster and a chisel-like biting surface develops.

What gives tooth enamel its hardness? Enamel is the hardest substance in the body, formed of calcium hydroxyapatite, a crystalline form of calcium phosphate. Tooth enamel is not crystalline in the same way that a crystal of quartz is crystalline. Teeth made of simple crystals would crack and chip under the high pressures developed in biting. Instead, the crystals of dental enamel are microscopic and extremely long. The crystals may be grouped in larger bundles or in sheets. These fit against each other the way sheets of wood fit against each other in plywood. The plywood principle of enamel structure gives it great resistance to cracking and chipping.

John Wahlert of Baruch College has compared the dental enamel structure found in different families of rodents. All rodents have a two-layered enamel. There is a thin outer layer, typically 20 percent of the thickness, and incorporating any pigment present in the incisors. Most of the hardness of the enamel is contributed by a thick, unpigmented inner layer. The inner layer shows the same fundamental "multiserial" pattern in guinea



Human and porcupine incisors in cross section (*top*) and longitudinal section (*bottom*). In both organisms, a softer, collagenous dentine forms the core of the tooth. In human teeth, the enamel layer completely surrounds the dentine. In the porcupine, enamel is laid down only along the front (labial) side. As a result, the porcupine incisor wears down to a chisel-like cross section. Drawing by Yenkang Ellen France.

pigs and porcupines. The multiserial pattern is common to all New and Old World Hystricomorphs.

Thus, the enamel in the white incisors of guinea pigs is built in the same way as the enamel in the orange incisors of porcupines. We must conclude that the twin properties of hardness (derived from crystalline structure) and crack-resistance (derived from layered construction) are what give tooth enamel its ability to hold the sharp edge developed in rodent incisors. If enamel ultrastructure alone can explain the sharp biting surfaces of rodent incisors, what alternate function might the iron pigments serve? The function of the porcupine incisor pigments remains a mystery.

Do porcupines have scent glands?

All mammals (with the possible exception of aquatic mammals) carry scent glands, which send odor messages to their own kind and, more rarely, to other species. Even the osmically challenged *Homo sapiens* has scent glands—the armpits—whose message we work hard to suppress with underarm deodorants.

Unlike humans, porcupines have a well-developed smell sense and have several kinds of scent glands. The scent glands found in all porcupines, in the Old World as well as the New, are the perineal glands. These are shallow, paired pockets located between the urethra and anus, and lateral to the midline. In North American porcupines, a large area of the lower back, the rosette, also functions as a scent gland. Unlike the perineal glands, the rosette transmits a signal to other species: "Warning, porcupine present!" Finally, there are the postulated nipple guides, guiding a nursing porcupette to the mother's nipples in the dark.

The perineal glands are classic skin glands, found not only in all porcupine species but in other Hystricomorph rodents as well. In 1922, the prominent mammalogist R. I. Pocock examined the external characteristics of a number of Hystricomorph rodents. He found perineal glands (which he called anal glands) in the Cape porcupine, *Hystrix africaeaustralis*, and in the Himalayan porcupine, *Hystrix brachyura*. He also found the glands in other Hystricomorph rodents including the coypu, Desmarest's hutia, the degu, the Patagonian mara, the guinea pig, the capybara, and the plains viscacha. But Pocock could find no glands in the North American porcupine. The specimen he examined had been preserved in alcohol. Perhaps the shallow perineal glands escaped notice by everting in alcoholic medium. Recently my coworkers and I have studied the histology and microbiology of the glands, using tissue from freshly road-killed animals.

The glands are found in both male and female North American porcupines. In males, the glands open as slits oriented perpendicular to the anal-

urethral axis. In females, where a vaginal closure membrane sits between the anus and urethra, the slits are oriented parallel to the anal-urethral axis. The perineal glands can be active (secretory) or inactive. The activity status of the glands can be determined by gently twirling a cotton swab in the perineal pockets. When active, the glands stain the cotton swab an amber color and give it a terpenoid odor. Inactive glands impart no stain or odor.

The perineal product, the amber-colored secretion with terpenoid odor, is not produced directly by the porcupine but by a rich bacterial community that occupies the glandular pockets. The bacterial community that characterizes the active state contains a small number of dominant forms, predominantly members of the phylum Actinobacteria, metabolic virtuosos capable of complex synthetic as well as degradative functions. For instance, Actinobacteria of the genus *Corynebacterium* convert the odorless secretions of the human sweat glands into pungent underarm odor. Other Actinobacteria are involved in the synthesis of antibiotics and in the degradation of complex macromolecules as well as oil and other hydrocarbons. The same genus of bacteria plays a prominent role in porcupine perineal glands.

The products of the perineal glands are disseminated by anal dragging, where the porcupine "paints" a projecting surface such as a branch with a small amount of perineal secretion. The painting is accomplished by wicks of hairs (osmetrichia) that sprout from the perineal openings. These hairs are firmly anchored to the bottom of the perineal pocket, and they have a ruffled surface that collects the odorant substance.

Shadle, Smelzer, and Metz found that in captive North American porcupines, males engaged in anal dragging more often than females. Likewise, Roberts, Brand, and Maliniak described anal dragging in a captive colony of Brazilian porcupines, *Coendou prehensilis*. Again, males dragged more frequently than females. The Cape porcupine, *Hystrix africaeaustralis*, as described by Rudi van Aarde, uses perineal dragging to mark territorial boundaries and favorite food sources. Massolo, Dani, and Bella have studied the chemistry of perineal secretion in the crested porcupine, *Hystrix cristata*. Based on the differences in chemical profiles between individual porcupines, they suggest that the secretions may be used in individual recognition. It appears that the glands serve a different function in the North American porcupine.

As noted earlier, the perineal glands of the North American porcupine cycle between an active and inactive state. What activates the glands? In males, active gland function requires fully descended testes. Of 25 males examined in New York State, 14 had fully descended testes and active perineal function, 10 had undescended testes and inactive function, and one had undescended testes along with active function. The statistical correla-

tion between descended testes and active perineal function is highly significant. Descent of testes in turn is controlled by body testosterone levels. In young males, the testes first descend when the animals reach sexual maturity at the end of their second year. Thereafter, the testes descend during the breeding season and are retracted back into the abdomen at other times.

Elevated testosterone also stimulates the microscopic sebaceous glands, whose product, the sebum, promotes the growth of the Actinobacteria that transform it into a pheromonally active product. (Sebum is the same oily substance that coats our hair). Thus, the hormonal state of the host porcupine activates the bacterial population that in turn generates the pheromone addressed to other porcupines. Actinobacteria disappear from the perineal glands when the androgen (male hormone) levels decline.

How about females? The active perineal glands of female porcupines house the same Actinobacteria-dominated microflora found in males, and glandular ultrastructure is similar in both sexes, with microscopic sebaceous glands lining the perineal pockets. Moreover, it is the androgens that constitute the hormonal trigger for perineal activity in both sexes. Androgens responsible for sebaceous gland activity in females are derived from the ovary and adrenal glands.

There is evidence that in North American porcupines, the perineal glands play a role in reproduction. Activation of the glands in males takes place when the males enter breeding condition. In females, the glands are activated in late summer and fall, as the females likewise enter breeding season. The fact that the testosterone surge in males lasts longer than the weak androgen surge in females may explain the observation that males spend more time anal-dragging than females do.

Another observation points to the reproductive role of the perineal glands in female North American porcupines. At the peak of the mating season, when males are guarding females in trees, the males have been observed carefully sniffing the branch where the guarded female has been resting. Sometimes the male gently nudges the female to move so he can sniff her resting spot.

The behavioral function of the perineal glands requires much further study. Studies in the wild are complicated by the fact that anal dragging in the tree canopy is hard to distinguish from normal movement in the branches. This is why most observations of anal dragging have been made on captive animals. Both captive and wild animals need to be studied further before the messages being sent by these enigmatic glands are teased out.

How long does it take a porcupine to digest a meal?

Passage, or transit, time is the length of time between an animal's swallowing its food and the excretion of the residue in the feces. For the North American porcupine, transit time has been measured by Felicetti and coworkers as 38 hours for particulate foods and 57 hours for liquids.

These times would be in the normal range for humans but are longer than expected for an animal in the porcupine size range. Many factors, both dietary and anatomical, influence transit time. One of the most important of these for the porcupine is the presence of the caecum, an important digestive organ at the junction of the small and large intestines. The caecum is a fermenting chamber where anaerobic bacteria and fungi break down complex food molecules such as cellulose and lignin, allowing the animal to extract useful energy from its low-nutrient, high-fiber diet of foliage and inner tree bark. The microorganisms of the caecum need time to do this work. A caecum is found in all New and Old World porcupines, in other rodents, and in herbivores in general. In humans, the caecum is reduced to the relatively small appendix.

Transit time for solids varies with the food item. Felicetti and coworkers speculate that the measured time of 38 hours for willow leaves may represent a minimum; longer transit times may be necessary for other food solids.

Van Jaarsveld has shown that transit time in the Old World Cape porcupine is notably faster, despite its larger body size: about 23 hours. This porcupine's diet of bulbs, tubers, and roots is easier to digest; hence, transit time can be reduced.

Do porcupines suffer from old-age diseases?

For old-age diseases to show themselves, an animal must first achieve old age. Unlike most wild animals, porcupines often achieve old age in wild-animal terms under natural conditions. I have estimated maximum life expectancy at 25 to 30 years for the North American porcupine. Others have shown that it is several years longer for Old World crested porcupines. This is sufficient time for old-age diseases to manifest themselves.

In most animal species, sick individuals are quickly removed by predators: a lame rabbit becomes a dead rabbit when spotted by a fox. But its excellent quill defense allows even a lame porcupine to survive an attack. The life of "Squirrel," a North American porcupine who lived to age 21 in the wild, was documented by radiotelemetry. In her last year, she was often unable to climb trees she had once climbed regularly to feed in. When she died a natural death the following winter, she was carefully examined.

The physical examination suggested good overall health, with a high body weight and a stomach filled with food. But her skeleton spoke otherwise: she was suffering from osteoarthritis in both arms. On one arm the heads of the radius and ulna (lower arm bones) were deformed. On the other arm, several metacarpals (bones of the palm) were fused with three wrist bones. When alive, she must have experienced great difficulty in flexing her wrists—the reason she had been unable to climb trees. The old porcupine also had dental issues. One of her molars was worn so far it had not only lost its grinding surface but was in danger of eroding down to the roots.

A better overview of old-age problems in porcupines can be gained by examining museum collections. For example, the National Museum of Natural History (Smithsonian Institution) in Washington, D.C., holds over 1,200 specimens of the North American porcupine.

Many skulls in the collection show dental wear far more severe than that seen in 21-year-old Squirrel. For instance, one skull, from Alaska, shows grinding surfaces remaining only on the premolars and third molars. The first and second molars are worn down to the gum line. Another porcupine, also from Alaska, shows all eight upper cheek teeth heavily worn, with teeth on the right side worn to the gum line. A third individual, from the Yukon, shows particularly heavy tooth wear on the lower jaw, where the cheek teeth have lost their grinding surface and all premolars and molars are affected. The animal must have macerated its food by a strange kind of rocking motion of its jaws. (For an example, see color gallery 1, page 5.)

But in contrast with old humans, none of the jaws of old porcupines showed missing teeth. From what we know, porcupines in the wild do not develop cavities!

Wendell Dodge, reporting on Massachusetts porcupines, found cancers of various organs. Thus, porcupines in old age develop many of the same old-age diseases observed in humans: osteoarthritis, tooth wear, cancer. Not observed in old porcupines are neurologic defects such as Parkinson's disease or epilepsy. Such diseases would be incompatible with survival in free-living porcupines.

Chapter 3

Porcupine Colors

What color are porcupine quills?

The quills of the larger porcupines—the Old World *Hystrix* and *Atherurus*, and the New World *Erethizon* (eastern subspecies), *Coendou prehensilis*, and *C. bicolor*—are black and white or brown and white, though individual animals with all-black and almost all-white quills are also found. In the western subspecies of the North American porcupine, the animals look yellowish-brown. The yellow-brown color comes from the guard hairs, which are longer than the quills and give the animals a deceptively furry appearance.

Among the small porcupines of South America, quills are typically yellowish or whitish with brown tips or brown bands, or all black. The details of quill color patterns are important when distinguishing related species. For instance, Robert Voss and Maria da Silva, in describing two new porcupine species from South America, paid special attention to the color patterns of the quills. They compared their new species, *Coendou ichillus* and *C. roosmalenorum*, with two related, previously described species, *C. pruinosus*, and *C. vestitus*.

Voss and da Silva noted that all four species have two kinds of quills: (1) the normal body quills, with sharp, barbed tips; and (2) bristle quills—longer, thinner, barbless quills that end in a thin filament. They found that *S. vestitus* could be differentiated from the other three species on the basis of color patterns of bristle quills, as shown in the table. The remaining three species could be differentiated on the basis of body quill color patterns. In this case, quill types and color patterns alone distinguish all four species, but the authors went on to describe and compare nine other distinguishing characters.

Identification of four South American porcupine species, genus *Coendou*, from quill color patterns

Species	Bristle quills	Body quills
C. vestitus	Bicolored	
	Long, dark tips	
C. pruinosus	Tricolored	Some head quills tricolored
	Long, pale tips	Short, dark tips
C. ichillus	Tricolored	Some head quills tricolored
	Long, pale tips	Long, dark tips
C. roosmalenorum	Tricolored	All quills bicolored
	Long, pale tips	Very short, dark tips

Clearly, this kind of close, careful analysis will not be always possible in the field, where the animal is in a tree and the observer on the ground. But there is one South American porcupine that it may be possible to identify in the field: the stump-tailed porcupine. Unlike all other South American porcupines, its quills have white bases tipped with brown or reddish bands. The fact is noted in its Latin name, *Coendou rufescens*, where *rufescens* means "reddish." This porcupine stands out among South American porcupines in general. In addition, the animal's tail is proportionately the shortest among South American porcupines, measuring only 40% of head + body length.

Is there a reason for coat color patterns in porcupines?

Coat colors in animals can serve a number of important functions. Vulnerable animals like snowshoe hares have coat colors that blend with the background, to make them less visible to predators. The snowshoe hare, which is brown during the warm months, turns white in the winter, along with the changing background. Predators may likewise have coats that blend with the background, the better to ambush their prey. On the other hand, well-defended animals like coral snakes and skunks carry coat colors that make them more conspicuous and intimidating to potential predators.

Coat colors may also act as signals within a species. Thus, the bright colors of male scarlet tanagers attract females during the breeding season but fade to yellow-dun when out of season. In many primates such as baboons, macaques, and chimpanzees, females signal receptivity by pink swelling of the genital region.

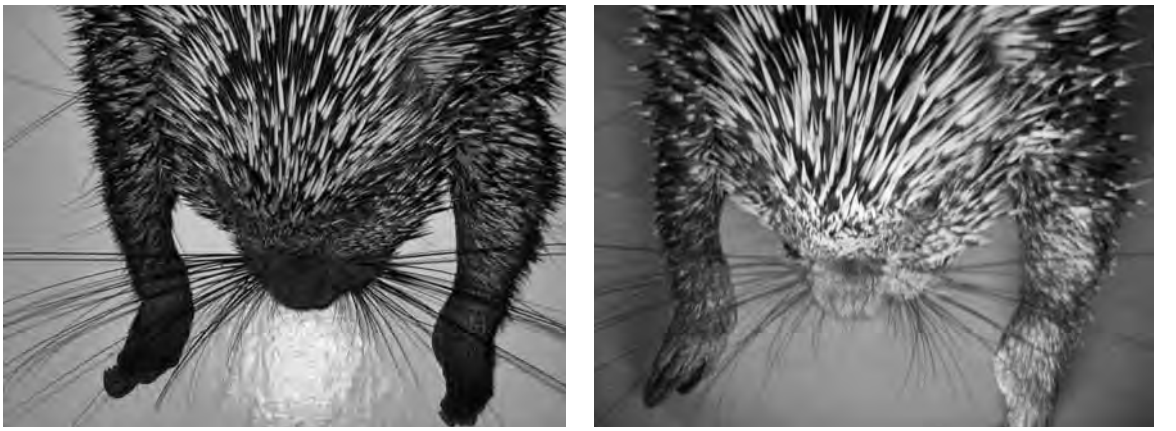
Most porcupines are well-defended animals, potentially dangerous to their predators. Their coat colors do not usually blend with the surroundings, as does the fur of the snowshoe hare or the feathers of a ruffed grouse.

To the contrary, typical porcupine coat colors, like the coat colors of skunks or red efts, stand out against the background and provide a warning to potential predators. Porcupines are active primarily at night, so the warning signal must also be visible at night. In most porcupines, the signal is a black and white contrast. In many South American porcupines, it is a dark brown–pale yellow contrast.

The North American porcupine shows a white chevron on its back that continues onto the tail and a white tuft on top of the head, set off against surrounding dark-colored quills. The white parts of the quills that generate the signal fluoresce under ultraviolet (UV) light: they contain a brightener that makes them lighter in the dark. Juveniles, who lack an effective quill defense, do not have the warning coloration; their tiny quills are hidden under a long black fur and guard hairs.

In Brazilian porcupines (*Coendou prehensilis*), white quills are massed around the head, and the white tips of the dark body quills seem to fly off in all directions like sparks from a fire. The body quills that generate the porcupine's warning signal are not themselves physically dangerous. They are too long and thin to penetrate the flesh, and their white tips lack quill barbs. But their threat message is not an empty one. Deeper in the pelage of the back and sides, and plainly exposed on the top of the head, the animal carries sharp, barbed quills. During a threat display, the porcupine may raise the midback quills, exposing their white bases. The white regions of

Warning color in the North American porcupine. Seen from the back, the porcupine presents a black and white contrast. There is a white chevron on the back and tail, and a white cap on the head, set off against a dark body. The black and white signal, directed to mammalian predators, is visible at night.



The head of a Brazilian porcupine, *Coendou prehensilis* (museum specimen), in visible light (*left*) and in UV light (*right*). The white quill tips fluoresce because they contain brighteners. These quills are meant to be visible at night, and form part of the porcupine's warning coloration. Museum specimen in American Museum of Natural History.

these quills carry brighteners just as in *Erethizon*; they fluoresce strongly under UV illumination. Quill fluorescence is seen in other New World porcupines as well.

The Old World crested porcupine (*Hystrix cristata*) has alternating black and white bands in the long quills of the back. The Himalayan porcupine (*H. brachyura)* shows massed white-tipped quills in the back, set off against black foreparts. Brush-tailed porcupines (genus *Atherurus*) carry a cluster of white rattle quills at the tip of the tail; the rest of the body is black. In all of these species, the white parts of the quills are fluorescent, suggesting a mechanism for enhanced visibility in the dark. Even the white erectable crest of the Cape porcupine, *Hystrix africaeaustralis*, is fluorescent under UV illumination. The erected crest adds to the illusion of size in this already large animal.

A number of hairy dwarf porcupines from Brazil (*Coendou insidiosus*, *C. roosmalenorum*, *C. spinosus*) violate the dark-and-light rule when viewed at rest. A thick fur layer hides their quills; the fur lacks a large-scale pattern. However, quill erection reveals the yellow or white bases of the quills and generates a dark-and-light contrast. The small thin-spined porcupine (*Chaetomys subspinosus*) likewise shows no color contrasts when at rest, with the dun color derived from its quills. All of these not-so-formidable porcupines have surface coloration that allows them to blend with their background while at rest.

Do porcupine colors change with age?

For the first few months of life, North American porcupine young are entirely black. Both their quills and their body fur are black. Their black

coats blend in with the normal hiding places of the porcupettes—under tree slash, under root tangles, at the back of rock crevices. They develop the white contrasts toward the end of their first summer of life, in parallel with their ability to defend themselves.

For the rest of porcupines' long lives, their coat colors change very little. In the North American porcupine, individuals may differ in the melanin content of their quills and hair. Some individuals are pure black and white, others are dark brown and white. These color variants remain stable within any individual and do not change with age.

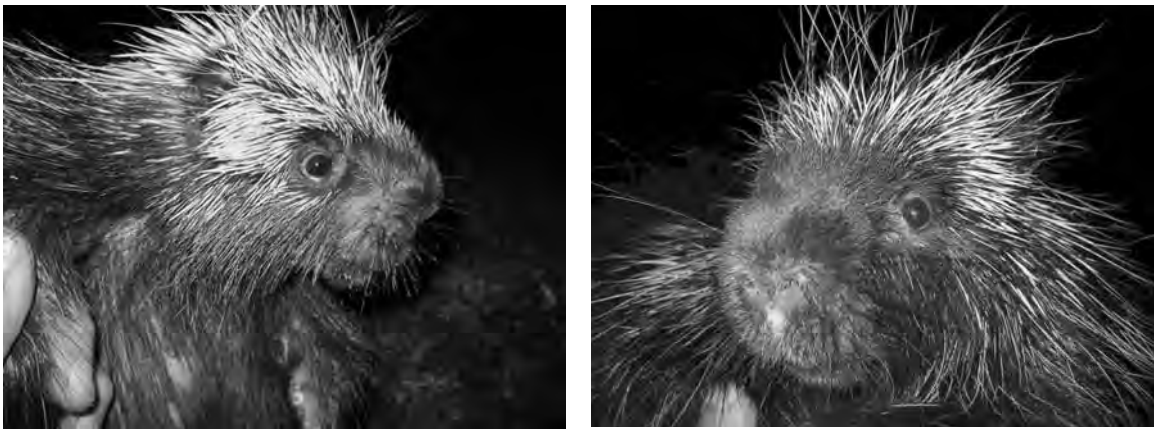
When very old (25+ years), North American porcupines develop their equivalent of the white hair of elderly humans. Their muzzles and areas around their eyes turn white. The muzzle and face are not covered with quills; what changes color is the facial fur.

Porcupettes of South American species begin their lives furry. The thick, reddish fur hides the quills even in species like the Brazilian porcupine, which as an adult has little or no fur under conspicuous quills.

How does fur color indicate that a female porcupine is lactating?

In the North American porcupine, the belly fur of males and nonlactating females is dark brown to black. But in lactating females, a narrow band of fur behind each nipple is bleached a light brown. The bleached

North American porcupine mother defending her baby. Mother and porcupette have put their heads under a rock outcrop. The mother's quills show the black and white warning coloration. The baby, carrying tiny quills, is almost entirely black. Its first instinct is to hide, not to advertise.



Head shots of young and old North American porcupine females. The two-year-old female and first-time mother (*left*) has a shorter, more shallow muzzle than the aged female (*right*), who is 14 years old and still giving birth every spring. The patch of white on her muzzle is one indication of her advancing age.

area stretches from the nipple towards the tail. The mother sits up during a nursing session, with the baby nursing against her chest. Presumably droplets of escaping milk or milk degradation products flow downwards and bleach the fur. The bleaching is permanent and persists until the following spring, when all fur is lost in a molt. The most likely bleaching agent is hydrogen peroxide, formed during the oxidation of milk sugars by fungal enzymes. (See color gallery 1, page 7.)

How can mother's milk serve as a bleaching agent? Milk of all mammals contains free sugars. Although the most abundant milk sugar is lactose, free glucose and galactose are also present. When these are oxidized by fungal enzymes such as glucose oxidase and galactose oxidase, the bleaching agent hydrogen peroxide is formed. The fungi providing the oxidase enzymes are from genera such as *Penicillium* and *Aspergillum*, which are widespread in nature and might be found on the mother's fur.

Do the bleached areas around the nipples help the baby find the nipple in the fur? If they do, the visual signal would be muted at night, when most nursing takes place. A possibility worth investigating is that the same milk sugars that give rise to the bleaching agent may also generate an odor cue that would serve as a more effective nipple guide in the dark. Fresh milk is almost odorless. But small amounts of milk left around the nipple would be subject to bacterial and fungal action. One of the products of such milk degradation is a class of compounds called lactones (cyclic esters). Lactones can impart burnt, fruity, stale, or coconut-like odors to stored milk products. Some of the microorganisms responsible for lactone formation include *Candida* and *Saccharomyces* yeasts and *Penicillium* and *Cladosporium*

mycelial fungi. Such tiny odor sources around the mother's nipples might help the baby find them in the dark.

Are albino porcupines found in nature?

Without offering any supporting data, Donald Spencer estimated that 1 out of 50,000 births in the North American porcupine produces an albino. Albino porcupines are also known among Old World crested porcupines. As discussed further, while the incidence of albinism is low, the 1 in 50,000 estimate is almost certainly too low. The low frequency of albinos in nature suggests strong selection against these mutations.

While different forms of albinism are known, all involve defects in melanin production. Melanin is needed for retinal development, and albinos show loss of visual acuity and other visual defects. Because porcupines are nocturnal animals that depend more on their senses of smell and touch, the visual impairments need not be lethal.

In porcupines, melanin is also required for optimal quill function. Melanin hardens the keratin protein of quills by cross-linking the keratin molecules much as sulfur cross-links latex molecules in vulcanized rubber. In the North American porcupine, quill tips are black even on largely white quills, and the tips typically carry one-way barbs. In albino porcupines, the black tips are gone or reduced to the vanishing point, and so are the one-way barbs.

To quantify the difference, I compared 10 quills from the back of a normal porcupine with 10 quills from an albino porcupine in New Hampshire. I measured the length of the barbed region at the tip of each quill. In normal porcupines, barbs covered 7.9 mm of the tip. In albino quills, the barbed region extended only for the first 2.35 mm of the tip region. The difference is highly significant and means that albino quills are less effective defense weapons than normal quills.

A further factor working against the albino, particularly during its first year of life, is that it is highly conspicuous and therefore more likely to attract a predator's attention. Again a saving factor could work for albino porcupines: porcupines defend each other, whether albino or normally pigmented, in the sense that they carry a species-specific warning odor. If the albino porcupine's warning odor remains intact, it may survive on the reputation of its better-armed conspecifics.

These compensation factors may be so effective in the North American porcupine that some albinos may reach adult size and live long enough to reproduce. A suggestion that albino porcupines may sometimes breed comes from the work of Dodge in western Massachusetts. He trapped or otherwise collected 214 porcupines. Two of these were albinos, a ratio far

Head shot, North American male porcupine. The white quills on top of the head are more pronounced than those on the female and constitute a secondary sexual characteristic, but with considerable variability from individual to individual within each sex.

too high to ascribe to independent mutation, thus suggesting an albino had reproduced. While the Dodge study makes Spencer's estimate of 1 in 50,000 statistically untenable, the study's sample size is too low to fix an alternate ratio.

An even higher incidence of albinos comes from the practice of Karen McElmurry, a wildlife rehabilitator in York, Maine. She receives a steady stream of porcupines in need of rehabilitation. In 2009, one of these was a juvenile albino. In 2010, she received three juvenile albinos, all from a 20-mile area. Two of the 2010 porcupettes had been mauled by predators, one severely, hinting at the higher risks encountered by such animals in the wild.

The high incidence of albinos in the area suggests several possible scenarios. One is that at least three albino females in the area are breeding with at least one albino male. (Porcupines produce one offspring a year.) An alternate possibility is that the breeding porcupines are not albinos but carry the gene for albinism as a recessive trait. Such animals are normal-colored and are said to be carriers. When two carriers mate, they can produce three kinds of offspring: albinos (¼ of offspring), carriers (½ of offspring), or normal, wild-type progeny (¼ of offspring). To produce the three albinos observed, a carrier male or males would have to mate, on average, with 12 carrier females (12 × ¼ = 3). Either scenario suggests that the albino gene is widely distributed in the local population.

Why do porcupines glow under a black light?

Porcupine quills glow under UV illumination for the same reason that newsprint, writing paper, and starched shirts glow: they contain brighteners. Brighteners are compounds that absorb ultraviolet light and emit part of it in the visible spectrum. As a result, normally white colors become extra-white. The brighteners of North American porcupines can be extracted from quills with solvents such as methanol, and they move readily in thin-layer chromatography. This suggests that they are small molecules.

Brighteners are present not only in the quills of North American porcupines, but also in South American *Coendou* species and Old World *Hystrix* and *Atherurus* species. The reason is probably the same for all: the white or pale-yellow portions of the quills appear brighter in contrast to their dark surroundings and serve as warning signals, even at night.

The principle of enhancing a white signal by adding brighteners is present in many animals beyond the porcupine group. For instance, the striped skunk, *Mephitis mephitis*, carries a V-shaped area of white fur on its head and back. This conveys a message to its predators that the skunk is well protected. The skunk's white fur glows under a UV light. By contrast, the white fur of a white dog serves no warning function and does not glow under a UV light.

In nocturnal skunks and porcupines, the white signals work at night and are directed at would-be predators. But nocturnal white signals can also be used intraspecifically, in contexts other than warnings. For example, the spiny rat, *Proechimys simonsi*, is a ground-dwelling species with brown fur above but a white belly that fluoresces brightly under UV light. Louise Emmons of the Smithsonian Institution, who has studied the species, observes that when two spiny rats meet, they use their bellies in social signaling (i.e., for personal communication).

This raises the question, not yet investigated, of whether any porcupine species use all or part of their white pelage as more than a warning to predators. Are there any social contexts where white body parts may be on display? North American porcupines show subtle variation in coat colors, some between the sexes, some between individuals. Thus, males have a more pronounced white patch on top of their heads. Does this signify anything to the females?

Chapter 4

Porcupine Behavior

Are porcupines social?

All porcupines live within social constraints, though perhaps only the Old World porcupines live in family groups. Even porcupines that lead solitary lives are acutely aware of the presence of other porcupines and react to them in specific ways.

Among North American porcupines studied in New York, females are territorial and exclude other females from their ranges but allow males to wander freely. Males interact amicably with local males but battle males outside the local group. Local males may also battle each other for access to females during the mating season. These porcupines are solitary except for mother-infant pairs and male-female couplings during the mating season. If forced, porcupines can share winter dens. The solitary life is perhaps imposed on the North American porcupine by its scarce food supply. The summer foliage it eats comes disproportionately from rare tree species scattered widely in the forest. Females defend such resources within their own territories; the widely scattered feeding trees could not support a herd of porcupines.

But while scarce resources are incompatible with herd living, there are countervailing factors that promote cooperation among porcupines. One example is the multigenerational task of creating a browsing forest around the winter den. Porcupines in the northeastern United States surround their winter dens with trees that are pollarded—"pruned" of the upper branches—through the work of successive generations of porcupines. The trunks of these trees are typically short, and the canopy sprouts a thick growth of thin-barked, highly edible branches that are immediately

North American porcupine "witch trees" around den under rock outcrop. These sugar maples have been pollarded on top, resulting in broom-like growth of thin-barked branches that make for easier winter feeding. The development of such trees requires the work of generations of porcupines.

distinguishable from the surrounding forest. These patches are referred to as witch forests. Old World crested porcupines likewise modify their environment, thus making the area more suitable for future porcupine generations.

Besides the change in surrounding forest, the dens themselves are modified over many years as the stone floor is coated with layers of insulating sawdust-like deposits derived from decomposed porcupine droppings. Another area of indirect cooperation is expressed in coprophagy. When a porcupine arrives at a new winter den and its associated browsing forest, it may ingest a piece of dropping from the previous occupant. The microorganisms ingested will serve as inocula to fine-tune the animal's gut microflora and adapt it to the local food supply.

These interactions do not fall under the normal definition of social behavior. Members of the porcupine population separated in time and space may benefit each other without direct contact or conscious agency.

Essentially nothing is known about the social structure of South American porcupines, but it should not be assumed that they mirror their North American cousin in social organization. Louise Emmons, in her field guide to South American mammals, observes that among both *Coendou bicolor* and *C. mexicanus*, adult pairs may be found denning together. And she reports four frosted porcupines, *C. pruinosus*, nesting together in the hollow of a rotten tree trunk.

Emmons has also shown that among Old World porcupines, the African brush-tailed porcupine (*Atherurus africanus*) lives in clans consisting of an average of three females and five to seven males each. The clans maintain well-defined clan boundaries. Dominance relationships within a clan appear to favor the females. The crested porcupines (*Hystrix* spp.) live as family groups: an adult male lives with an adult female (who tends to be

slightly larger) and their offspring of the previous few years. Though older daughters may be sexually mature, only the adult pair breeds.

Do porcupines fight?

Porcupines are by temperament gentle, unaggressive animals. Their reactions to would-be predators are purely defensive. Yet under specific circumstances, porcupines will fight.

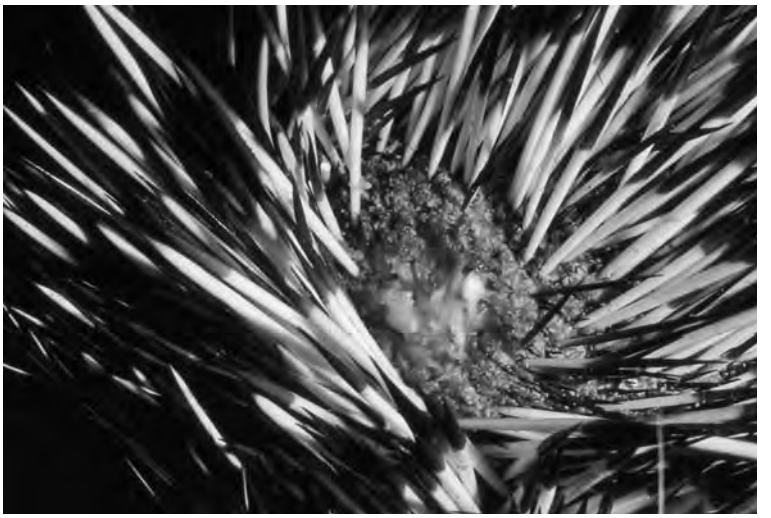
In North American porcupines, the animals doing most of the fighting are sexually mature males. The timing of battles between males is the porcupine mating season (early fall), and the object is mating rights with the females. When dominant males battle each other, they use every available weapon: quill strikes, teeth, and attempts to force each other out of the tree where the female is waiting. The results of such battles include ears bitten off, faces gouged, quills driven into the skin, and possible bone fractures or death if the animal is hurled out of a tree.

Battles between females are rare; they occur when one female encroaches on the territory of another. The females then grapple with each other, a lot of quills are lost (as evidenced by a thick scatter on the ground), and the intruder soon flees. Females almost never carry the kind of permanent wounds that so many males display.

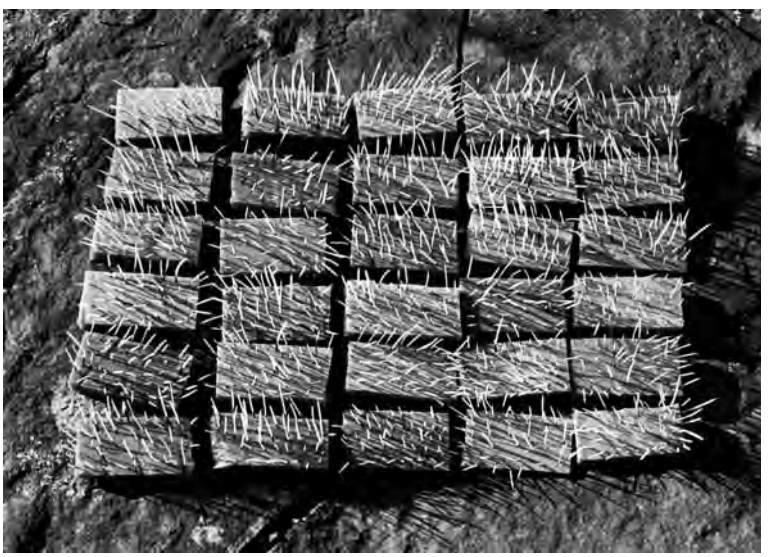
Battles have also been recorded between Old World porcupines. Louise Emmons found African brush-tailed porcupines living in clans that controlled individual territories. In one experiment in an artificial setting, a juvenile female was placed in a fenced enclosure with males. The resident males almost immediately attacked and killed her. It is not clear that the same outcome would have been observed under natural conditions, where the female would have had free choice of movement and would have been able to flee.

Rudi van Aarde of the University of Pretoria observed that in the Cape porcupine, *Hystrix africaeaustralis*, adults of both sexes care for the young, and males accompany their juvenile offspring on foraging expeditions, where they protect them against would-be predators and other porcupines.

Hystrix can engage in vicious fights in zoo settings, with animals using their fearsome incisors to tear out patches of one another's skin and flesh. Again, there is no reason to believe these fights would occur in the porcupines' natural settings, where the porcupines live in family groups and avoid the territories of other groups.



Missing quills on the back of a North American porcupine. The animal was a male and had an injury on top of its right hip, possibly a result of a predator attack. New quills are sprouting all around the edge of the wound.



Battle quills. The 1,474 quills shown were collected at the site of a battle between three North American porcupine males over a female. There were probably many other quills lost in the leaf litter.

Do porcupines bite?

Porcupines may bite each other during battles, but when humans handle porcupines, the animals almost never bite, even when the animal being picked up is untamed. Porcupines' instinctive defense is to use their quills, either by tail-slapping as in the North American porcupine, or by the use of body quills, as in other porcupines.

When porcupines battle each other, the large incisor teeth can be put into sometimes deadly use. Among North American porcupines, males may bite each other without getting quills embedded in their mouths, as would a dog. It is not clear why porcupines may use their teeth on each

other but not on their potential predators. Perhaps there is a difference between defensive (fear-driven) and offensive (anger-driven) behaviors. It might be interesting to see how a mother porcupine disciplines her porcupette (although Roberts and coworkers note that Brazilian porcupines, *Coendou prehensilis*, do not discipline their young).

Do porcupines play?

Play in animals is a serious activity. When a kitten chases a crumpled paper ball around the room, it is perfecting motor skills that will later help it chase a mouse in the grass. Two puppies wrestling and play-biting may be establishing a dominance relationship while learning to use their canines. A deer fawn running and leaping is acquiring agility and escape behavior.

Play is primarily a pleasure of the young, and this is true of porcupines as well. Albert Shadle, who kept a colony of North American porcupines, describes young animals engaging in defense play: putting the head under some projection, erecting the quills, jumping up and down, and flicking the tail. Other observers describe twirling on all fours. All this is done when the animal is alone, with no threat present. In the wild, the motor skills learned in such activities may someday save the animal's life.

A favorite group game described by Shadle is wrestling. One animal would attack another, followed by several minutes of twisting, holding, biting, and much whining and scolding by the animal under attack. Then the roles would reverse as the victim became the attacker and play continued. This behavior would appear to be rare in the wild, since North American porcupines are born alone and do not grow up with brothers and sisters.

Multiple births are possible in the Old World crested porcupines (litter size of 1 to 3), so group play may be a more natural phenomenon in these animals. Erna Mohr, who raised crested porcupines at the Berlin Zoo, describes four of the animals, their quills lightly spread, hopping in a circle "like a group of dancing girls in petticoats." And Kathleen LaMattina of the Bronx Zoo describes an adult female Indian crested porcupine as the "most exuberant animal" she has ever met. The porcupine loves getting sprayed with a water hose, jumping into boxes, and rolling around the cardboard tubes her treats come in.

The African brush-tailed porcupine, like the crested porcupines, lives in family associations and has been described as playful in zoos. The playfulness apparently extends to animals living in the wild, as described by Gerald Durrell during an expedition to Cameroon, West Africa. Brush-tailed porcupines like to den in natural caves. Durrell described a Cameroon forest porcupine cave with an internal 8-foot-high rock wall that sloped gently to form a natural slide. He found that the slide was "worn smooth by the

constant passage of the porcupine bodies or bottoms." The tracks in the sand indicated that the porcupines "scrambled up to the top of this slope, slid down, walked around, climbed up again and slid down once more. They must have been indulging in this game for a number of generations, as the rock face was worn smooth as glass."

How smart are porcupines?

In purely anatomical terms, the porcupine would not appear to be a candidate for academic honors. Its cerebral cortex does not show the elaborate surface folding visible in the brains of intelligent animals such as wolves, whales, or elephants. (Folding of the cerebral cortex indicates a large surface area and therefore a high neuronal density.)

Yet porcupines perform surprisingly well on certain tests of intelligence. The American psychologist L. W. Sackett tested North American porcupines for the ability to learn complex mazes. The porcupines learned quickly, at about the same rate as primates, and could remember the route when tested 100 days later. This is perhaps not surprising, because when navigating to its food or rest trees in the forest, the porcupine must learn and remember a kind of maze.

Similar experiments have not been done with other porcupines, but the superb competence demonstrated by the Indian porcupine, *Hystrix indica*, in avoiding traps set by angry farmers (whose potatoes and carrots the porcupine loves) suggests learning ability.

How do porcupines communicate?

North American porcupines are surprisingly vocal. During the fall mating season, a porcupine's scream can slice like a siren through the night. The screams are directed at other porcupines: males battling for a female or females rebuffing overeager males. When porcupines are irritated by one another but emotions have not reached a fury stage, they produce high-pitched squawks. Such squawking is commonly heard when porcupines are forced to share a winter den. Even when the animals are deep in the ground in a rock den, their squawking can be clearly heard outside.

At the other end of the loudness spectrum, a baby porcupine may produce a soft "mmm" sound while calling for its mother. When the mother fails to appear and the baby's distress grows, it may cry much like a human infant, expressing unmistakable distress. Babies produce a happier sound during nursing, when the baby and the mother "sing" to each other in a responsive way.

Besides their use of vocal signals, North American porcupines can also communicate by odor, a sense richly developed in mammals. It appears that these porcupines have two olfactory language systems. One set of signals is reserved for members of other species (usually would-be predators). The message conveyed is "Watch out! I am a porcupine!" The other is an intraspecies olfactory message system used to convey information to other porcupines and involves porcupine urine as well as secretions of the perineal glands.

Visual and auditory warnings back up the porcupine's olfactory warning to would-be predators. Visually, the porcupine presents a black-and-white contrast along its back and the top of its head, constructed with black and white quills. For its auditory warning, it chatters its teeth. Finally, after erecting its quills, it releases a unique warning odor associated only with the North American porcupine.

The source of the warning odor is the skin of the rosette, an area of the lower back. The rosette is quill-covered but sparsely furred, thus enhancing its odor-dispersing capacity. The warmth of the skin helps volatilize the odorant, and its nakedness allows rosette quills to pick it up and disseminate it. Rosette quills are specially modified for odor dispersal, being more extensively barbed than other quills and having greater barb overlap. These features increase their surface area and allow them to carry greater odorant loads.

The warning odor is produced not by the quills but by the near-naked skin below. Rosette skin is richly supplied with microscopic sebaceous glands—the same gland type that lines the pockets of the perineal glands. These glands are primarily associated with the follicles of the underfur.

The compound responsible for the warning odor has been isolated and its structure determined by Guang Li, David Locke, and myself. The structure is a 10-carbon cyclic molecule called delta decalactone. Delta decalactone can exist in two isomeric forms: *R*- and *S*-isomers. The porcupine produces only *R*-delta decalactone. The two isomers have different smells and different optical activities (they rotate polarized light in opposite directions). *S*-delta decalactone smells like coconut; only *R*-delta decalactone smells like defensive porcupine. By producing a pure compound, the porcupine has sharpened its message: nothing else in the forest smells like porcupine.

Other porcupines likewise send warning messages to potential predators. Many South American *Coendou* species make flashy displays of bright-tipped or bright-banded quills. According to Gaston Gine, the thin-spined porcupine of Brazil, *Chaetomys subspinosus*, whose quills are less formidable than those of other New World porcupines, generates a warning signal by tooth chattering. The tooth chatter of *Chaetomys* is more prolonged than that of its North American cousin. The Brazilian porcupine, *Coendou*

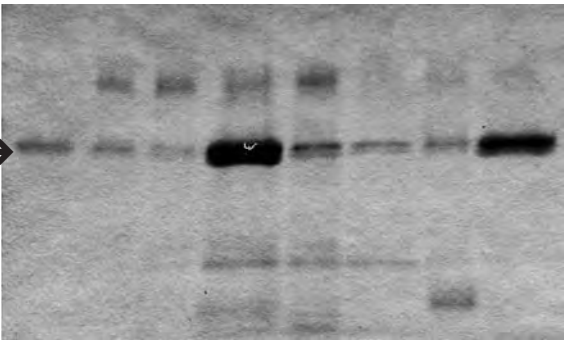
Rosette area of adult porcupine. The quills are far more developed than those of a juvenile, but the bare skin can still be seen below the sparse underfur.

Skin surface of the North American porcupine (epidermis removed). Directly below the three cut quills (*top*) are clustered pits from which the paraspinous hairs emerged. On the bottom are scattered pits from which the underfur emerged; these are also the openings from which a sebaceous substrate carrying the warning odor reached the skin surface. SEM photo by David M. Chapman.

prehensilis, likewise chatters its teeth during hostile interactions and prior to attack.

The Old World brush-tailed porcupines can vibrate their distinctive tails to produce a rattling sound. Old World crested porcupines also have rattle quills located at the tips of stubby tails. Vibration of the tail produces a loud warning sound. Crested porcupines add to the warning by flaring their quills and erecting their manes to add the illusion of great body size. They also stamp their feet, chatter their teeth, and produce grunting sounds.

All these sights, sounds, and smells are directed at other species—the potential predators of the porcupines. In addition to such messages to members of other species, porcupines also communicate with each other. Though vocal signals play a role in this communication, the principal modality used is smell, a sense well developed in porcupines.



Porcupine urinary proteins separated by gel electrophoresis. Here, urine samples from eight porcupines are placed in adjacent lanes and separated according to size (with the smallest proteins on top). All lanes contain a protein (*arrow*) identified as albumin. Dimitri Matassov, personal communication.

In the North American porcupine, intraspecific (porcupine-to-porcupine) odor messages are most often sent via urine. The urine of this porcupine species may be specially adapted to carry odor messages. Unlike human urine, porcupine urine carries a significant amount of protein. The protein is albumin, whose normal mammalian function is to transport free fatty acids via special binding sites. Though the possibility remains to be proven, porcupine urinary albumin may serve a similar carrier role for odorant molecules.

The role of proteins in odorant (pheromone) transport is illustrated by the urinary proteins of mice and rats. In these animals, urine contains about 3% protein (higher than the level in North American porcupines), and the proteins carry pheromones with important roles in reproductive behavior, such as induction of estrus in females. As shown by M. V. Novotny, the protein prolongs and protects the pheromonal signal.

In the North American porcupine, urine signals are used in at least two different ways. First, drops of urine are used to mark den entrances and the bases of feeding and resting trees. The urine signals are clearly visible in winter, when the droplets stand out against contrasting snow. There is evidence that marker urine is applied year-round at the base of resting trees and feeding trees. Urine marks may help the animals locate these resources in the dark, when they are foraging, and they may also serve to warn other porcupines away. When two porcupines find themselves in close proximity, as when sharing a den, the urine marks grow large and ostentatious.

A second mode of urine signaling in the North American porcupine involves males' spraying females with urine during the mating process. While direct evidence is lacking, the urine signal probably works in porcupines as it does in mice and rats, to induce estrus in the female. It should be stressed that the hypothesis of urine signaling in porcupines awaits experimental confirmation.

Crested porcupines of the Old World also scent-mark their territories and feeding sites. But the medium used is not urine; rather, according to Rudi Van Aarde, it is the secretions of the perineal glands.

Feeding tree (*left*) marked by urine in the snow trail of a North American porcupine. More typically, only a few drops of urine are left by each feeding tree.

Do porcupines hibernate?

No porcupine, either in the Old World or the New, has evolved the capacity to hibernate. Of all the porcupines of the world, the North American porcupine might have benefited most from this behavior, since it spends its winters in extreme cold with low food availability. Its recent evolutionary divergence from its tropical cousins in Central and South America may not have allowed time enough to develop this possibility. It continues active foraging through the long North American winter, partially sheltered by a den in the ground or in a hollow tree.

How fast can porcupines run?

Running speed is exceptionally low in New World porcupines but higher in Old World porcupines, particularly the crested porcupines. Cottam and Williams have determined that the North American porcupine is putting forth maximal effort when running about 2 mph (3.2 km/h). This is a speed that humans can easily exceed. A runner running a 4-minute mile is moving at 15 mph (24 km/h). Porcupines make up for their lack of speed by a surprising agility and quickness of movement. The low speed of the porcupine results from a combination of very short legs, plantigrade locomotion, and low muscle mass. The North American porcupine does not depend upon running for escape. At the first opportunity, it climbs a tree or enters a crevice or available den.

Old World crested porcupines are considerably larger than the North American porcupine, and size translates into greater running speed. Like all porcupines, the crested porcupines walk by plantigrade locomotion, in which the entire sole of the foot contacts the ground. All fast-running

mammals move either by digitigrade locomotion (only the toes touch the ground, as with the cheetah, which can run at 70 mph, or 112 km/h), or unguligrade locomotion (only the toe tips touch the ground—e.g., the pronghorn, which achieves speeds of 60 mph, or 96 km/h). Even with its plantigrade locomotion, the crested porcupine is nevertheless described as fleet of foot. It achieves its speed by running on its toes, just as plantigrade humans do. Both crested porcupines and brush-tailed porcupines can outrun a human being. But like the North American porcupine, the crested porcupines do not depend on speed for escape; they depend on their formidable quills and the protection offered by their deep dens.

How do porcupines climb trees?

Among porcupines, the tree-climbing specialists are the New World porcupines, who climb trees for food, shelter, and rest. The Old World crested porcupines have very limited tree-climbing ability—they depend on underground roots, tubers, and corms for food.

North American porcupines can climb onto the outermost branches of the tallest trees, using five appendages to get there: four limbs and a tail. All of these appendages play an important role in the tree-climbing process. The fingers of the front limbs are elongated compared with the fingers of their terrestrial hystricomorph cousins (though not as elongated as the fingers of primates). The fingers and toes have long, curved claws that find purchase in furrows and crevices of the tree bark. Then the well-developed arm and leg muscles propel the animal higher. The tail, which carries stout bristles on the underside, is pressed against the tree trunk to prevent back-sliding.

When a porcupine reaches the thin branches of the upper canopy where use of its claws is no longer practical, it can keep going by using its footpads. The footpads are covered with tuberosities that increase the friction between branch and footpad. By gripping a branch between the soles of its hind feet and stabilizing itself with its tail, a porcupine can free its front limbs to snag nearby branches for food.

South American porcupines such as the Bahia porcupine, *Coendou insidiosus*, also use four limbs and the tail in climbing, but with certain differences. For the first third or so of its length, the underside of a *Coendou* tail carries stiff bristles. These are used in ascending or descending a tree trunk much as the tail of *Erethizon* is used. But because the tail of a South American porcupine is thinner and less muscular, its climbing contribution is less robust.

More importantly, the long tails of typical South American porcupines serve as grasping (prehensile) organs. The dorsal side of the tail tip carries a high-friction, footpad-like tuberosity that curls upward to encircle a

North American porcupine in top of a sapling. To climb saplings, porcupines use the friction soles of their hands and feet, while keeping the tail firmly pressed to the trunk. Porcupines often feed in saplings because the thin bark can be harvested in a single pass.

Front footpad of a North American porcupine. The pebbled, high-friction surface of the footpad allows the animal to grip branches and tree bark. The four long curved claws assist it in tree climbing because they can be inserted into bark crevices; they can also be folded back across the footpad to hold branches and other small objects.

branch. All porcupines of genus *Coendou* have a prehensile, upward-curling tail. A porcupine can use it to hang itself from a branch with tail and hind limbs, using the forelimbs to forage for fruit and leaves. Its tree-climbing prowess is further enhanced by extensions of the frictional surfaces of the hind footpads, making South American porcupines superb arborealists.

Lima and coworkers describe similar tail-use behavior in the thin-spined porcupine, *Chaetomys subspinosus*. The animals climb to the top of the feeding tree, rest on their hind limbs, and anchor their tails around firm branches before beginning to feed.

Do porcupines fall out of trees?

Only New World porcupines climb trees regularly, so the possibility of falling out of a tree applies primarily to this group. For the North American porcupine, falling out of trees is a major cause of accidental death. Investigators in Quebec, Massachusetts, and New York have all described porcupine deaths from falls.

Falls seem to arise from a mismatch between the weight of the animal and the load-bearing capacity of the small branches in the tree canopy where the animal forages. A special danger is posed by bigtooth and quaking aspen (*Populus grandidentata* and *P. tremuloides*), both of which are important summer foods of the porcupines. The branches of aspens are brittle and may snap under the weight of a porcupine.

The bodies of porcupines killed or injured by falling are not easy to discover unless the animal was wearing a radio collar. Evidence of falling comes from the high incidence of healed fractures in porcupine skeletons held by museums. In 37 skeletons I have examined, 35% showed healed fractures. Among a control group of 45 woodchuck skeletons (an animal of comparable weight but not commonly engaged in tree-climbing), only 6.7% showed healed fractures.

The healed fractures in porcupines included breaks in the long bones of the arms and legs, the hip, and shoulder blades. While all these animals must have been temporarily incapacitated by their injuries, they survived long enough for the fractures to heal, a testimonial to porcupines' powerful quill defense. In the much smaller sample of animals that died as a result of their falls, the injuries involved fractured skulls and broken vertebral columns. Such injuries produce instant death or paralysis.

How prevalent are tree fall accidents among South American porcupines, who likewise forage in tree tops? Because of lighter body weights and the additional protection provided by prehensile tails and prehensile extensions of the footpads, fewer accidental falls would be predicted among this group. A close look at museum specimens confirms the prediction. In an examination of 32 wild *Coendou* skeletons at the American Museum of Natural History I found only one healed fracture, or a 3% incidence, compared with the 35% incidence in *Erethizon*. The difference is highly significant and demonstrates the protective value of a prehensile tail to an animal

Female North American porcupine foraging for sugar maple buds high in the canopy. Because the buds grow at the tips of small branches, the porcupine lives dangerously.

that spends time in trees. When the evolutionary ancestors of *Erethizon* gave up the prehensile tail, they paid a heavy price in tree-use safety.

How can I tell whether a tree is being used as food source by a porcupine?

North American porcupines live in forests and get essentially all their nutrition from trees. But other animals share the forest with porcupines and may at times make use of the same food sources.

Black bears climb beech trees in the fall to harvest beechnuts. Since bears are much too heavy to venture out to where the nuts lie clustered, they stay near the center of the tree and bend the branches back till they snap. The bear can then pull the branch back to the center of the tree and remove the nuts. A kind of giant nest is created.

Porcupines feeding on beech nuts are less destructive: they move out along individual branches as far as they can go, then cut off the branch tips with clusters of nuts, remove the beechnuts, and let the cut twig tips fall to the ground. The cut twigs, called nip twigs, show clean angular cuts at the base.

Another food consumed by black bears and porcupines alike is apples. In North America, apples are not native forest trees, but they do infiltrate the forest edges from seedstock spread by a variety of wild animals. As in beech feeding, bears snap large apple branches to bring the outlying fruit into reach. Porcupines cut off only small terminal twigs to access the apples

A porcupine nip twig. To eat the leaves at the tips of small branches, North American porcupines nip off the terminal branch, consume the leaf blades, then discard the naked branch with its petioles. The freshness of any remaining leaves gives an indication of time elapsed since feeding.

and let the nip twigs fall to the ground. White-tailed deer are also apple lovers. But they must be satisfied with fallen fruit or fruit stripped from low-lying branches. Because deer lack upper incisors, they don't leave the neat angular cuts on branches that porcupines do.

In the summer North American porcupines feed on tree leaves. Such feeding is seldom obvious from looking at the canopy. Instead, porcupine feeding is revealed by nip twigs which accumulate on the ground below feeding trees. The nip twigs have had their leaf blades removed, with petioles (leaf stalks) left behind. Tree species commonly used by porcupines in the eastern United States include aspens and linden in the summer, and ash and beech in the spring. In early spring, before leaves have budded out, porcupines use the nip-twigging technique to feed on the buds of sugar maple. The buds are surgically excised; the rest of the twig is discarded.

In winter, with trees standing bare, porcupines feed on the inner bark (phloem). Most such feeding is done up in the canopy, and trees are left with shiny white branches as underlying wood is exposed. The white streaks in the canopy can be seen from a distance and indicate porcupine feeding. Beavers, who also feed on tree bark, do not climb trees for their food. Porcupines use a wide variety of trees in their winter feeding mode: sugar maple, beech, elm, oak, aspen, linden, and other hardwoods.

Porcupines also consume the inner bark of softwoods such as ponderosa pine, yellow pine, Douglas fir, and spruces. Hemlock is a great favorite in the east, but because hemlock bark is well defended by tannins, porcupines feed almost exclusively on the needles of this tree. Needles are harvested by the classic nip-twigging technique: a terminal branch is neatly cut, the needles are removed, and the unused mass is dropped to the ground. There, it is often scavenged by deer.

The nip-twigging technique does not appear to extend to South American porcupines, who remove fruit and leaves directly from their food tree branches. This may be made possible by their prehensile tails and often much smaller body weights.

Old World porcupines may feed on tree bark during the dry season, when normal underground foods become less available, but because these animals do not climb trees to feed, the debarked areas extend no higher than a porcupine's height above ground level.

Chapter 5

Porcupine Ecology

Which geographic regions have the most porcupine species?

Generally, more porcupine species are found in tropical regions of the world than elsewhere. The North American porcupine is the only species found in areas where the winters bring snow and ice, and a restricted food supply.

The New World tropics are the most species-rich in porcupines. Robert Voss recognizes 15 species of New World porcupines. Fourteen of these have a tropical distribution, ranging from central Mexico to southern Brazil. The tropics of Central and South America in which porcupines are found are almost all forested. These are the habitats to which these species' prehensile tails and footpads have best adapted them. Mammalogists believe that more South American porcupines remain to be discovered.

Do porcupines migrate?

Unlike caribou or wildebeest, porcupines do not make long-range, seasonal group journeys in response to changes in food supply. But porcupines do make long-distance, one-way journeys from their natal ranges (home ranges of birth) to the home ranges they will occupy as adults. The process of juvenile dispersal has been studied in only one porcupine species, the North American porcupine.

North American porcupines have a dispersal pattern that is uncommon among mammals. In most mammal species, the predominant dispersing sex is the males, who leave their natal ranges while females stay on the natal

range to adulthood. In porcupines, this pattern is reversed. At the end of their first summer, females leave their mothers and the territory of their birth and travel long distances to establish new territories, from which they will never return.

The consequence of this sex-biased juvenile dispersal is that porcupines avoid inbreeding. A young female will not be at risk of mating with her father or brothers. The chance of a stay-at-home son mating with his mother is deferred: it takes around four years for a male to reach sexual maturity and adult weight, and battle his way up to dominance rank.

Adults may also disperse, though infrequently. The predominant dispersing sex in adults is the males, which may disperse when frustrated in their struggle for reproductive dominance. Instead of engaging in endless battles, an adult male may choose to leave his place of birth and embark on a long journey to a more hospitable environment. Such journeys are risky, and instead of success, the outcome may be death.

Can several porcupine species live together in the same area?

In not sharing its species range with any other porcupine, the North American porcupine is somewhat anomalous in the porcupine world. In Central and South America, and in the Old World, two or more porcupine species are often found coexisting in the same area.

Robert Voss and Maria daSilva, of the American Museum of Natural History and the Amazonia Museum at Manaus, respectively, have observed that in both the eastern and western Amazon regions, two porcupine species may be found sympatrically (living in the same area). Where such sympatric pairs are found, one is a large porcupine, the other a small one. In the western and northern Amazon, the large species is the bicolored porcupine, *Coendou bicolor*; and the small species are the dwarf porcupines *C. ichillus*, *C. pruinosus*, and *C. vestitus.* In the eastern and southeastern Amazon, the large species is the Brazilian porcupine, *C. prehensilis*, while the small porcupines are *C. insidiosus*, *C. nycthemera*, *C. spinosus*, and *C. roosmalenorum*. In each case, the small porcupines have a small species range and the large ones, larger ranges.

The coexistence of large and small mammals—porcupines, antelopes, primates, and so on—is a well-established principle in the ecological literature. The large and small species can live in the same area because they occupy different ecological niches (ways of making a living) and therefore do not compete. What those niches may be for the New World porcupines is still completely unknown.

But for porcupines, the separation of ecological niches does not always

depend on size differences. Two small porcupines occupy the same forest in southeastern Brazil. These are the thin-spined porcupine (*Chaetomys subspinosus*) and the Bahia dwarf porcupine (*Coendou insidiosus*), who live together in the Atlantic Forest. The population densities of the Bahia porcupine are larger than the densities of the thin-spined porcupine, in part because the Bahia porcupine can persist in more degraded habitat. Where the two species coexist, individuals can literally rest in the same trees with no sign of antagonism.

What allows the two species to live together without competition? Perhaps the thin-spined porcupine, which diverged early from other South American porcupines, is so different from the other porcupines that it can subdivide the arboreal folivore niche by factors other than body size, such as quill structure, defense strategy, and diet breadth. We don't know.

Different-sized porcupines also coexist in the Old World. The medium-sized African brush-tailed porcupine, *Atherurus africanus*, is sympatric with the large Cape porcupine, *Hystrix africaeaustralis*, in the eastern part of its range, and with the equally large crested porcupine, *H. cristata*, in the west. The brush-tailed porcupine feeds on fallen fruit from forest trees; the *Hystrix* species dig for their foods and can live in more savanna-like environments.

In Asia, sympatry has been documented between the large Himalayan or Malayan porcupine (*Hystrix brachyura*) and the medium-sized Asiatic brush-tailed porcupine, *Atherurus macrourus*. These overlap in a range from south-central China in the north to the Malay Peninsula in the south. At the southern end of their common range, they reach the northern range of the small long-tailed porcupine, *Trichys fasciculata*. Miura and coworkers have photographed *H. brachyura* and *T. fasciculata* feeding on the same fallen fruit in Malaysia. Kitamura and coworkers used a similar technique in southern Thailand, with similar results. The basis of niche separation in these species is poorly understood, but differences in foraging strategies probably contribute to the separation.

Are there porcupines in the desert?

Yes and no. North American porcupines have been described from deserts in Idaho, Nevada, and Texas. However, the animals are not evenly distributed in these deserts; instead, they concentrate around water sources with brushy or treelike vegetation. Desert porcupines do not typically feed on cactus but, rather, on vegetation such as buffaloberry and willow (Great Basin desert, Nevada, described by Sweitzer and Berger) and river hawthorn and ground vegetation (Idaho desert, described by Craig and Keller). Desert porcupines tend to be larger than those in forest habitats—23

pounds (10.5 kg) on average for adults in the Idaho desert as opposed to 11 pounds (5.1 kg) on average for adults in Massachusetts hardwood forests.

Old World Cape porcupines have a wide ecological tolerance and may be found in forests as well as semidesert, savanna-like habitats. In their arid habitats, their feeding activities (debarking of trees in the dry season, disturbance of seedlings by digging) produce a level of disturbance that prevents establishment of the forest and perpetuates the savanna, as described by deVilliers and coworkers.

The same broad ecological tolerance is shown by the crested porcupine, *Hystrix cristata*, and the Indian crested porcupine, *H. indica*. The crested porcupine is absent from extreme desert, such as the Sahara, but its species range in Africa forms a great crescent around that desert: the animal is found to the east in Ethiopia and Tanzania, curves west through Nigeria and Guinea, then north to the edge of Mauritania. After a break, it is found again from northern Morocco to Tunisia. All the crested porcupines dig for their food. When the desert is so extreme that no roots and tubers exist, the porcupines likewise cannot survive.

How do porcupines survive the winter?

Winter survival is most difficult for just one porcupine species—the North American porcupine, whose species range extends to far northern Canada and Alaska. This porcupine has multiple adaptations for winter survival. First is a winter pelage with excellent insulation properties derived from a mix of three hair types: a thick fur, long guard hairs, and the familiar quills. Piloerection (elevation) of the quills and guard hairs can be controlled separately. The three hair types working together provide better insulation than would any one layer. Nevertheless, winter survival is not assured, especially for juveniles. Their little bodies lose heat rapidly and may lack sufficient fat reserves to keep warm.

The fur layer for North American porcupines is renewed yearly: it is the only layer to undergo an annual molt (shedding of hair). Thus, the porcupine is never without quills. The fur is molted in the spring, with the advent of a high-protein diet that helps the animal grow new fur. (Fur is itself made of protein.) At the end of the molt, quill-free regions such as the cheeks, the areas around the eyes, the belly, and the limbs appear bare and pink. A new fur layer has regrown by summer's end. It may be so long and thick that it hides the quills.

Winter insulation is also provided by a subcutaneous fat layer, laid down in late summer and fall. The fat layer serves the additional purpose of storing reserve food calories. By the end of winter, it is depleted.

Another winter adaptation is the use of a den. North American porcu-

North American porcupine following the spring molt. The belly, which has no quills, is pink and almost bare on this young male. By end of summer, it will be covered by a fresh coat of fur.

This adult North American porcupine casts a look back as she enters her den, which reaches more than 12 feet into the rock outcrop and offers substantial winter protection.

pine dens are not excavated by the porcupines themselves (unlike some of the burrows of their Old World cousins). Preferred dens are rock crevices that reach deep into the earth and moderate both ambient temperature extremes and wind chill. Where rock dens are scarce, porcupines may use hollow trees or logs. Rarely, a porcupine may spend the winter in a hemlock stand or other evergreen shelter, where climatic conditions differ little from conditions inside a den. But typically, porcupines spend most of the winter in their dens, emerging to feed for 4–6 hours a day, typically at night.

Winter foods available to the North American porcupine contain less protein, more fiber, and more plant defense compounds (toxins to deter herbivory) compared with spring and summer foods. As a result, porcupines lose body weight and deplete stored fat layers. Porcupettes are born in a seasonal surge when winter is over and the forest provides an abundance of high-nutrition spring buds and leaves. The porcupettes grow explosively during this window of opportunity. To survive the coming winter, they must lay down thick fur and subcutaneous fat.

The rapid seasonal growth of baby North American porcupines exceeds the growth rates of their South American cousins. This seasonality of growth and reproduction can therefore be considered another facet of winter survival strategy.

Do porcupines get sick?

The North American porcupine harbors a wide variety of parasites, including tapeworms, nematode worms, lice, ticks and mites, protozoa, and bacteria. The animal and its parasites are for the most part well-adapted to each other, and a porcupine with dozens of tapeworms, hundreds of lice, and tens of thousands of intestinal nematodes may present the picture of health. In fact, some of the so-called parasites may be mutualists, benefiting the porcupine as well as themselves. Microorganisms in the caecum help the porcupine digest complex carbohydrates; nematode worms in the same area may help regulate its internal sodium pool; and lice in its fur may help keep the fur clean.

Among the porcupine parasites that seem to have only a minor impact on their hosts are the large, highly visible ticks acquired by North American porcupines. These ticks are related to the microscopic mites that cause scabies. Although physically much larger than their scabies relatives, the ticks cause no distress to the porcupines. In the eastern United States, the common porcupine tick is *Ixodes cookei*, which also attacks woodchucks, raccoons, and other medium-sized mammals. Adult ticks attach to the belly and can swell to the size of a pea. The ticks do not transmit Lyme disease

Scanning electron microscope image of the porcupine tick (*Ixodes cookei*) mouthparts. The barbed hypostome anchors the tick in the skin of its host. Unlike the deer tick, this tick is not a vector for Lyme disease.

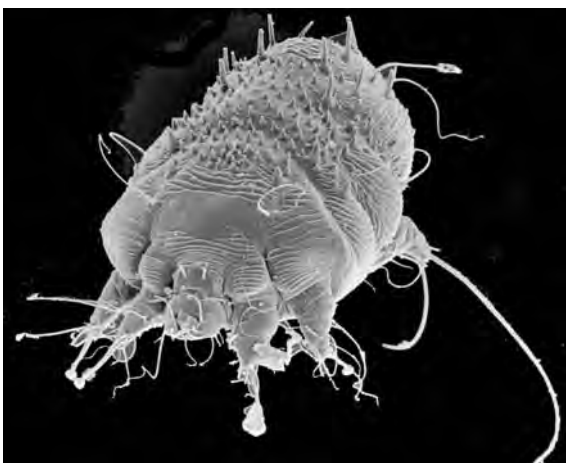
and have no visible effect on their hosts. They drop off after their tiny blood meal and disappear during winter.

Essentially every wild porcupine also harbors another group of parasites, the tapeworms. The most common forms on North American porcupines are *Monoecocestus americanus* and *M. variabilis.* Porcupines may host dozens of tapeworms, and they continually shed white proglottids with their droppings. Perhaps because the tapeworms are specialized for porcupines, they appear well adapted to their hosts. Even heavily infected porcupines show no sign of malnourishment or ill health.

In contrast, a number of porcupine parasites that appear to be recently acquired may bring serious illness or death to their host. A general ecological rule of host-parasite relationships is that parasites or disease organisms are most deadly at first contact. Thus, when Native Americans first encountered European settlers, the natives were decimated by the everyday diseases the settlers brought with them, not just smallpox and measles, but also the common cold. It is estimated that the preconquest Inca population of 17 million was reduced by 93% after the conquest. The Europeans suffered relatively little because over many generations host and parasite had

evolved mutual adaptations: higher immunity for the host, lower virulence for the parasite.

One example of a disease that appears to be new to the North American porcupine is the scabies mite (*Sarcoptes scabiei*). Though scabies is a disease of long standing, scabies mites are markedly species-specific. The strain that infects dogs, for example, cannot reproduce on human skin, though it may cause itching and skin lesions. The first observation of a scabies infection in a North American porcupine was made in 1958 by Payne and O'Meara in Maine. Since then, hundreds of cases have been reported in porcupines by veterinarians, wildlife rehabilitators, forest rangers, and others. The disease has spread widely from Canada in the north to Pennsylvania, New York, and Texas in the south, and east to the limits of the porcupine species range.



The scabies mite, *Sarcoptes scabiei*, burrows into the skin of the North American porcupine, setting up a violent scabbing response that typically disables and kills the porcupine. The mite shown in this scanning electron micrograph is an adult female. SEM photo by Louis De Vos.

Scabies infection in a female North American porcupine. The skin of the hind limbs and lower abdomen is crusted, cracked, and open to infection. The animal is unable to climb trees or move other than with great effort. If untreated, the disease kills its victim.

The origin of the porcupine strain of the scabies mite is unknown. The most likely mode of scabies transmission between porcupines is by den sharing or by sequential den occupancy, and the same mechanism probably spread the mite from the original host to the porcupine. Testing of this idea will require sequencing of *Sarcoptes* DNA from a variety of host organisms.

Scabies is a fatal disease in porcupines. The female mite digs a long burrow under the host's skin, laying eggs as she goes and dying at the end of the burrow. When the eggs hatch, the juvenile mites dig their own burrows back to the surface of the skin. The porcupine responds with scabbing and thickening of the skin that causes loss of the ability to climb trees and difficulty in walking. Fissures open in the skin, exposing inner organs. Death follows from infection and starvation.

The disease may be particularly deadly because the association between the scabies mite is a recent one. Other parasites of the porcupine have lived far longer with their host and may have evolved more gentle forms of association. The scabies mite that kills its host is likely to die in the process. The severity of the interaction, coupled with the solitary habits of the porcupine, limits the extent and duration of the epidemics.

Sorci and coworkers point out that a number of factors can influence the outcome of parasite-host interactions. Is the opportunity for transmission high or low? Does transmission primarily involve unrelated hosts or closely related ones such as mother and offspring? Only with the second alternatives do parasite-host interactions evolve in the direction of mutual accommodation.

Scabies is easily treated with a 1-minute dip in 1% malathion. The more widely used treatment with ivermectin will likewise cure the scabies, but will also affect the fetus if the female is pregnant and will cause the loss of caecal nematodes, which may compromise the animal's sodium retention ability.

Another parasite with potentially fatal consequences for porcupines is the raccoon nematode (*Baylisascaris procyonis*). *Baylisascaris* is not a threat to wild porcupines, which have little association with raccoons. Rather, it threatens porcupines in zoo settings or similar surroundings where the animals may be exposed to raccoon feces containing *Baylisascaris* eggs. The nematode is well adapted to raccoons, which tolerate it without visible harm. But when the eggs are ingested by the "wrong" host, such as a porcupine or a human being, the nematodes invade the brain, where they cause severe physical damage that leads to neurological disturbance and death.

While porcupines may suffer from viral colds and pneumonia, one pathogen the porcupine does not suffer from is the rabies virus. On the other hand, porcupines have been described with the symptoms of cancer.

Nevertheless, their high infant survival and long life expectancies testify to a lifestyle where disease is not a major threat.

How can you tell if a porcupine is sick?

With scabies, no veterinary background is necessary for diagnosis. The underside of the porcupine's body becomes covered with a thick, yellow-white encrustation that leaves the animal too crippled to carry on with daily travel and tree-climbing. The disease may be confirmed by taking a skin scraping and examining it under a microscope. The scabies mites will be visible as hairy, translucent arthropods (8 legs in adults, 6 in juveniles).

A raccoon nematode (*Baylisascaris*) infection that has progressed to brain damage will manifest itself with neurologic symptoms: gross lack of coordination, somnolence, loss or impairment of rear limb movement, head tilt, and pawing of the air. The *Baylisascaris* is a large nematode, and as it migrates through the brain, it causes progressive damage that culminates in death. Confirmation on autopsy requires the expertise of a veterinary pathologist.

The symptoms of a cold in a porcupine parallel those in a human: sneezing, coughing, and mucous discharge.

Caution should be exercised in diagnosing disease in porcupines. The animals are normally active during the night and may spend much of the day sleeping and immobile. A sleeping porcupine should not be mistaken for a sick porcupine.

Are porcupines good for the environment?

The practice of classifying animals as "good" or "bad" can be full of pitfalls. A recent example comes from the Australian island of Macquarie, located between Tasmania and the Antarctic. A number of bird species, some of them endangered, nest on the island. The island was also home to feral cats who preyed on the birds and their nests. It was decided to eradicate the cats. Bergstrom and coworkers describe the outcome. The cat eradication program began in 1985, with the last cat killed in 2000. But the result was ecosystem devastation. With the cats gone, the island's introduced species of rabbits and mice multiplied unchecked and destroyed much of the plant life that had supported the birds. So were the Macquarie feral cats good or bad for the environment?

There is a divergence of opinion about the environmental effects of porcupines. The North American porcupine feeds on tree bark during the winter. As a result, trees may grow crooked and misshapen; a few are killed outright. Because such porcupine damage is highly visible, the animal has

attracted the wrath of landowners and the timber industry. In the past, New England states offered bounties for porcupines killed. The bounties have all been discontinued, but many landowners still kill porcupines on sight; in many states the animals are not protected by any game laws.

Because porcupines sharply reduce their travel during winter, their tree damage is not spread evenly through the forest but is concentrated around their winter dens. In New York and New England states, trees in these locations grow up short and have misshapen ("witch tree") crowns (see the photos on pages 61 and 113). The witch trees are preferred winter feeding sites for the porcupines. But in the summer, the forest floor under the witch trees receives increased summer sunlight, causing development of understory plants. Such understory development favors a range of species, including ruffed grouse, white-tailed deer, moose, hares, mourning warbler, yellowthroat, and other forest birds and mammals. If the feeding trees are hemlocks, the dropped twigs attract hares and deer.

Beyond the effects of their winter feeding, porcupines also exert more diffuse, less visible effects on their forests as a result of nonwinter feeding. To feed on buds, leaves, and fruit, they prune their feeding trees by removing small terminal branches via the technique of nip-twigging. Pruning can increase the productivity of a tree much as pruning in apple orchards improves apple crops. The question regarding the porcupine's environmental impact therefore gets different answers.

A similar divergence of opinion exists on the question of the environmental impact of the Old World crested porcupines (genus *Hystrix*). Instead of climbing trees, the animals seek their food at ground level and below the ground. Crested porcupines like to visit potato, melon, pumpkin, and corn fields. For this reason, the animals are considered farm pests and are hunted relentlessly.

On the other hand, the feeding activities of South African Cape porcupines in the savanna is a form of disturbance that maintains the savanna ecosystem and prevents ecological succession to dry forest. They disturb the soil by digging and burrowing (with up to 3,460 diggings per hectare) and make trees more susceptible to fire in the surrounding scrub. The savanna ecosystem of the Cape porcupine is one of the richest in the world. Some of its inhabitants include impalas, steenboks, kudus, brown hyenas, lions, leopards, five mongoose species, warthogs, aardvarks, spring hares, hedgehogs, and a host of others. For all of these, the Cape porcupine is not a pest but an animal whose environmental impacts make it a pillar of the ecological community.

Wilby and coworkers summarize studies on the related Indian crested porcupine, *Hystrix indica*, in the Negev highlands of Israel. They point out that, like all herbivores, porcupines can affect their environment in two

distinct ways. One is by feeding interactions—consumption of plants and competition for food with other herbivores. The other is by ecosystem engineering—altering the physical structure of the environment in a way that affects living processes. Beavers, elephants, humans, and porcupines are all ecosystem engineers.

In examining the direct feeding effects of Indian crested porcupines, studies show that the animals have very little impact on the population dynamics of their food plants. Thus, for the porcupine food plant *Tulipa systola*, bulb consumption rates varied widely from year to year, with a maximum of 6% of bulbs consumed per year, but natural population replacement of tulips consistently compensated for the porcupine consumption.

In contrast, the physical changes to the soil surface as a result of porcupine diggings were important and long-lasting. The porcupines dug pits that persisted from several years to decades. During this time, the pits accumulated water and organic material, including seeds. As a result, pits contained eight times the plant biomass and twice the plant species numbers of undisturbed soil. The Indian crested porcupines are therefore classic ecosystem engineers, effecting physical and biological changes in their environment as a result of their foraging activities. The ecosystem effects of Indian crested and Cape porcupines are far more important than their direct feeding effects. The resulting increase in biomass and species richness makes their environment a little less desertlike.

What are the important porcupine predators?

For porcupines across the world, the important predators vary, but all have one important predator in common: humans. Human predation is overt in Africa and Asia, where porcupines are hunted and highly valued as game. In North America, the human impact is more indirect. Porcupines are killed secondarily as a result of road salting. North American porcupines are also managed by state fish and wildlife agencies through the reintroduction and release of the porcupine's deadly enemy, the fisher (*Martes pennanti*). When fishers become established in a porcupine habitat, the porcupine population can be reduced by 80% or more.

The fisher is a mustelid, related to weasels, martens, otters, and similar forms. Males weigh up to 12 pounds (5.5 kg), and females, up to 7 pounds (3.2 kg)—less than the porcupine. The fisher's success against the porcupine derives from two factors. First, the fisher is an agile tree climber. It can therefore follow a porcupine up its normal refuge. In this instance, an important defense mechanism used by porcupines is to position themselves on a branch with the tail facing the trunk. A fisher approaching from this direction will get a face full of quills.

The tracks of a fisher in the snow. When a fisher is running, its hind feet land in the impressions of the front feet, creating the two-by-two pattern shown here. Because fishers can travel more easily in the snow than porcupines, their predation success increases in winter. The walking stick on the right is 4 feet long.

A second reason for the fisher's success is that on the ground, it attacks an undefended region of the porcupine's body: the face. The face of a porcupine, like its belly, carries no quills. Powell has described a porcupine-fisher interaction. When taking up a defensive position, the porcupine guards its head by pressing it against a tree trunk or similar surface, and presents only its back and tail to its adversary. Exploiting its speed and mobility, the fisher circles around the porcupine, trying to bite its face. If the porcupine can't reach a safe location (a problem exacerbated by deep snow), the repeated bites to its face may weaken and disorient it to the point where the fisher can attack the porcupine's underside and kill it. It then consumes the porcupine by feeding from the chest and abdomen.

Not all fisher attacks are successful, nor are fishers immune to porcupine quills. A large male porcupine, weighing twice as much as the fisher, is probably immune to attack if it is not hampered by snow. But juveniles and females would be easily dispatched.

While the fisher is well-equipped to kill porcupines, typical porcupine densities are not high enough to sustain the fisher population. Fishers therefore expand their diet to include snowshoe hares, squirrels and small rodents, birds, and carrion. All these are more important prey for them than porcupines.

Another efficient carnivore of the North American porcupine is the

mountain lion (*Puma concolor*). Unlike the fisher, it does not try to avoid the porcupine's quills: it tolerates them. Mountain lions that prey on porcupines typically have dozens of quill tips embedded in their gums and elsewhere in their bodies, without apparent ill effect. Mountain lions have a limited tree-climbing ability, so a favorite hunting method is to climb below a porcupine in a tree and knock it to the ground. The porcupine is then quickly dispatched.

A chilling example of the effects of mountain lions on porcupines comes from the work of Sweitzer, Jenkins, and Berger in the Great Basin Desert of Nevada, who report that a population of 82 porcupines was reduced to just 5 animals over a 3-year span by mountain lion predation. The authors attribute the predation to the fact that mule deer, the normal prey of the mountain lion, had declined in the area. But since mountain lions are exceedingly rare and since the species range of the mountain lion no longer overlaps extensively with the species range of the porcupine, the mountain lion must be considered a far less important porcupine predator than the fisher.

Many other would-be predators— coyotes, bobcats, lynx, wolves, wolverines, and great horned owls—have been known to attack North American porcupines, but few pose a serious threat. Among the more obscure threats to the porcupine is the bull trout, *Salvelinus confluentus*, a large salmonid with a species range stretching from northern California to the Canadian Northwest Territories. Peter Cott and Neil Mochnacz of Fisheries and Oceans Canada report angling a bull trout in a stream of the Mackenzie Mountains of Northwest Territories that had four porcupine tail quills embedded in its upper lip. While the bull trout is a top predator known to include small mammals in its diet, Cott and Mochnacz do not believe the porcupine was an intended food item. They hypothesize that the porcupine was either swimming or fording the stream when the bull trout attacked it while defending its spawning ground, on which the porcupine had inadvertently intruded.

Who preys on the South American porcupines? The most formidable predators appear to be the large cats, like jaguars and ocelots. Minor predators may include snakes like boas. While young boas concentrate on smaller animals like rats and squirrels, there are records of adult boas killing porcupines. The intended victims can put up a fight.

A 2004 report from a Rio de Janeiro newspaper describes eight firefighters who had been called to remove a 7-foot boa from the back yard of a house in hills above the city. (Rio De Janeiro is surrounded by a large urban rain forest, part of the Atlantic Forest, that harbors monkeys, tree sloths, anteaters, and porcupines.) The snake had large black spines embedded in its head, and the firefighters believed it had entered the yard after a battle with a porcupine. Many inhabitants in Rio's outlying areas keep chickens

and ducks, which must have seemed more attractive to the snake after its porcupine encounter. The snake's captors removed the spines, treated its wounds, and released it back into the forest.

In the Old World, crested porcupines and brush-tailed porcupines are regularly sold in markets as bush meat. In addition, they are killed by farmers whose crops attract the porcupines.

Among native wildlife, the important porcupine predators are the large cats—lions and leopards as well as hyenas. Leopards kill many brush-tailed porcupines. Again, the porcupines have other plans. The large crested porcupines erect their manes and quills, making the animals appear larger than they are. They make a noisy display with rattling quills and foot stamping. Then they run backwards or sideways, trying to impale their enemies. The results can be devastating to the would-be predator. In 2006 in South Africa's Kruger National Park, a leopard was found dead by the side of the road near Satera Camp. The leopard had been pierced by dozens of quills from a Cape porcupine.

What possible mutualists live with porcupines?

North American porcupines are known as hyperparasitized organisms: they host an apparent excess of both internal and external parasites. Some of the disease-causing forms have already been mentioned (see "Do porcupines get sick?"). But there are many parasites that cause no disease symptoms and may in fact be mutualists, helping the porcupine.

Prime examples of such possible mutualists are nematode worms of the genus *Wellcomia*. Although most nematodes are microscopic, *Wellcomia* are giants among the nematodes, almost 1 inch (about 2 cm) long, and easily seen with the naked eye. *Wellcomia* are found by the tens of thousands in porcupines' intestinal tract and are often shed with the feces. Sometimes the body of a *Wellcomia* can be found stringing two droppings together.

Wellcomia in the North American porcupine are not distributed evenly in the intestinal tract but aggregate in the caecum, a stomach-sized sac at the junction of the small and large intestines. Besides playing an important role in digestion, the caecum serves as the porcupine's sodium pool. It is here that the porcupine stores the sodium it can draw upon through the winter months, when salt is not available. Do the *Wellcomia* nematodes have any role in maintaining the elevated sodium levels of the caecum? Their large body mass and high density, and their restricted location, differentiate them from other nematode parasites of the porcupine and give them the physical tools to manage sodium regulation. The question deserves study.

If the *Wellcomia* nematode does serve a sodium maintenance function,

it would function as a mutualist, not a parasite. And if there is a mutualistic relationship between porcupines and their nematode worms, that relationship should be conserved during evolutionary time. This is the situation observed. A study by J.-P. Hugot of the National Museum of Natural History in Paris shows that the North American porcupine is not the only one that harbors *Wellcomia* in its intestinal tract; other New World and Old World porcupines do so as well. The intestinal nematode species in the various porcupines are specific for each species, but all are members of the genus *Wellcomia*. Interestingly, DNA sequence analyses show that the evolutionary tree for the *Wellcomia* parasites mimics the evolutionary tree of their porcupine hosts. Both trees show an Old World branch, a New World branch, and an evolutionary connection between the two.

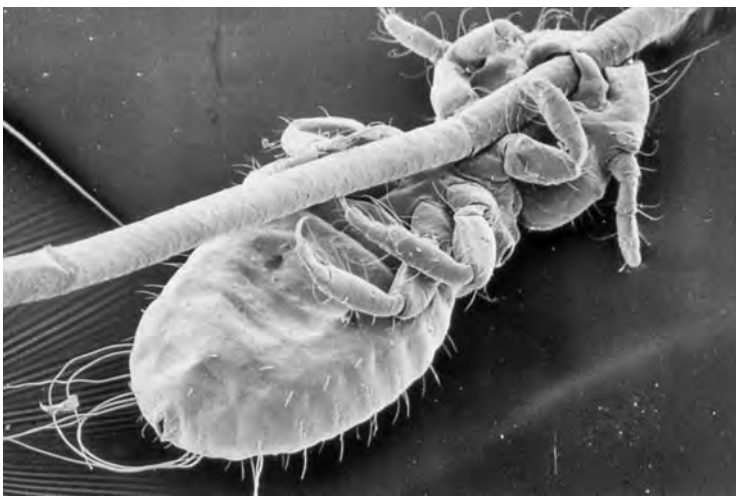
Another group of porcupine parasites is their lice. Most mammalian lice (including human lice) are members of the Anoplura, the sucking lice. They insert a stylet into their hosts and suck the blood, causing intense itching and discomfort. Lice of the New World porcupines are members of the Mallophaga, the chewing lice, which are predominantly found on birds. The chewing lice may be gentler on their hosts: they feed on skin cells and surface debris.

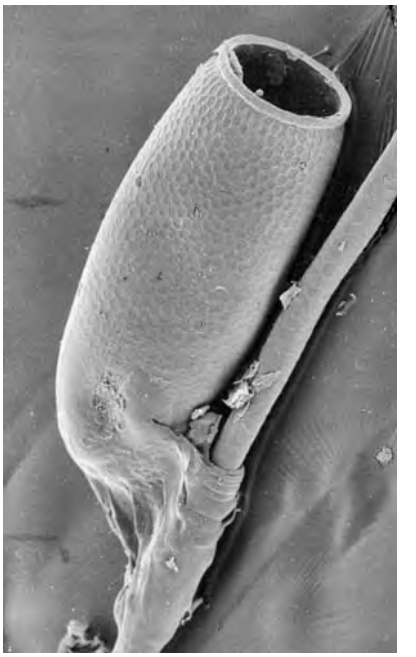
The louse of the North American porcupine, *Eutrichophilus setosus*, is an example. A typical porcupine may carry upwards of a thousand lice, yet the animal shows no discomfort and no inclination to use its long claws to scratch itself. Despite the large numbers of lice on the porcupine, only a few are visible on the surface. The rest stay deep in the fur layer, close to the warm skin, clinging to individual hairs (not quills).

The lice lack eyes yet can run quickly up and down an individual hair (*Eutrichophilus* means "good lover of hair"). The louse holds on by wrapping the front pair of legs around the hair while using the hind pairs for propulsion. The little animals can also hold on with their mouthparts, which hold the hair in a groove on the underside of the head. Because the tight contact of the mouthparts clears the hair of accumulated grease and detritus, the louse may be performing a cleaning function for an animal that cannot readily groom itself.

Eutrichophilus setosus is the only louse species found on the North American porcupine. South American porcupines of the genera *Coendou* and *Chaetomys* all carry *Eutrichophilus* lice. But in these cases, the work of Timm and Price shows that more than one louse species can be found on a porcupine.

In 1936, F. L. Werneck at the Instituto Oswaldo Cruz in Brazil made a study of the lice of the Paraguay dwarf porcupine, *Coendou spinosus* (for Werneck, *Sphiggurus villosus*). He found three lice species on a single animal: *Eutrichophilus cordiceps* (abundant), *E. minor* (less abundant), and *E. cer-*





The porcupine louse, *Eutrichophilus setosus*, may exhibit a commensal (neutral) or mutualistic (beneficial) relationship with its host. *Left*, Porcupine louse on a North American porcupine. The insect holds onto the hair with its mandibles and moves up and down with the aid of its six feet. *Right*, The egg of a porcupine louse, called a nit. To prevent being detached from the body by host's grooming, the egg is securely attached to a porcupine hair. SEM images by David Chapman.

colabes (scarce). How did three species of related lice coexist on the same host animal without interbreeding? Werneck shaved a porcupine, exposing its naked skin, and observed acts of copulation among the remaining lice. Lice copulate somewhat like humans, lying head to head and clasping each other, but with the female on top. There is a 2-hour precopulatory stage during which the lice lie pressed against each other, immobile. This allowed Werneck to identify the species of both partners. He found no attempts at hybridization: all lice mated only with their own species. As with *Erethizon*, Werneck observed that the lice caused no distress to the porcupines.

Eutrichophilus lice are not found on other South American rodents, including the related Caviomorphs. This suggests they may be specifically adapted to life on porcupines. The *Eutrichophilus*-porcupine association probably evolved in the New World because the lice are absent from all the Old World porcupines.

Do porcupines compete for food with other vertebrate herbivores?

For the North American porcupine, the quick answer would be both no, and widely. While there are no significant competing mammal foliage feeders, some porcupine foods are valued by other northern animals. Autumn mast crops such as acorns and beechnuts are important to a large group of herbivores and omnivores, including deer, bears, wild turkeys, deermice, and squirrels. Porcupines, bears, and squirrels feed on mast while it is still up in the trees; most of the other mast eaters feed on the ground. Feeding on mast in trees lowers its availability on the ground, putting porcupines in direct competition with tree feeders and indirect competition with ground feeders. However, the population density of porcupines is low enough that their competition pressure would typically be slight as well as seasonally limited.

In Central and South America, local porcupines face a wider circle of potential feeding competitors. Estrada and Coates-Estrada studied possible feeding competition between arboreal mammals in Mexico. Besides the Mexican porcupine (*Coendou mexicanus*), the study included primates (howler and spider monkeys), two opossum species, two squirrel species, and two carnivore species (kinkajous and ring-tailed cats). Fruit-eating bats, present in the forest, were not included in the study. They found that the *C. mexicanus* diet was 20% leaves and 80% fruit. The leaf trees recognized as palatable were the same ones used by howler and spider monkeys.

Estrada and Coates-Estrada described factors that limit competition between the arboreal mammal species. The animals foraged at different levels in the canopy: the monkeys fed primarily in the upper canopy level, the porcupines in the middle layer, the opossums in the lower levels and on the ground, and the squirrels in all levels equally. The animals selected different foods in the trees: the howler monkeys fed on leaves and fruits; the porcupines overwhelmingly selected fruits and immature seeds; and the opossums and carnivores fed on a mixture of fruits, insects, and small invertebrates. In addition, the animals fed at different times of day. The primates and squirrels fed during the day; all other mammal species fed at night. This subdivision of the arboreal feeding niche by Mexican mammals is summarized in the table. Estrada and Coates-Estrada noted that while the different foraging patterns enumerated above may reduce competition between mammals, fruit production in a tropical forest may be erratic. When fruit production fails, as from excessive rainfall, a general famine may result, and the fruit eaters may be forced to compete across species lines.

Another study of tree-feeding mammals, by Charles-Dominique and coworkers, compared the feeding behavior of the Brazilian porcupine (*Co-*

Feeding separation between nine arboreal mammal species in a tropical rain forest at Los Tuxtlas, Mexico

	Forest level (%)[a]			Food part consumed (%)		
Species	L	M	U	Leaves	Fruit	Other
Primates						
Howler monkey	0	30	70	48	50	2 (flowers)
Squirrel monkey	0	30	70	20	80	0
Carnivores						
Kinkajou	0	60	40	0	52	48 (small invertebrates)
Ring-tailed cat	0	60	40	0	40	60 (small invertebrates)
Porcupines						
Coendou mexicanus	0	75	25	18	82	0
Squirrels						
Sciurus deppei	30	40	30	5	95	0
S. aureogaster	30	40	30	10	90	0
Opossums						
Didelphis marsupialis	60	25	15	0	38	62 (small invertebrates)
Philander opossum	50	30	20	0	52	48 (small invertebrates)

Source: Based on Estrada and Coates-Estrada 1985.

[a] L = lower (0–10 m), M = middle (10–20 m), U = upper (>20 m)

endou prehensilis) with potential mammal competitors in French Guiana. The study focused only on night-feeding mammals that forage in trees. Besides the porcupine, these included two other rodent species (a spiny rat and a rice rat), four opossum species, and the kinkajou. Fruit-eating bats, present in the area, were not studied. The authors separated the species according to whether they foraged in the lower level of the forest (0–5 m) or the upper level (5–30 m). Three opossum species and the rice rats foraged primarily in the lower level; all the others foraged in the upper level.

Dietary choice formed another facet of feeding separation. The Brazilian porcupines fed largely on immature fruit and their seeds, which they could extract even from hard fruits. The spiny rats also fed on immature fruit and seeds but obtained them from entirely different tree species. The opossums and kinkajou fed on the pulp of ripe fruits, foods that were extremely low in protein. They supplemented their fruit diet with protein-rich insects and small vertebrates.

Do porcupines undergo population cycles?

In a cyclical population, population densities rise and fall over time in a predictable way. Well-known examples include the 10-year cycle of the snowshoe hare in Canada. The hares are prey of the lynx, whose own population rises and falls in response to prey abundance. Other mammals exhibiting population cycles include northern rodents such as lemmings and voles and the more widely distributed muskrat. The common characteristic of such cycling populations is their restriction to high-northern ecosystems, where community structure is simplified. Herbivores have few choices in terms of food species, and carnivores have few prey options. In addition, all cycling herbivores have a high rate of reproduction, allowing for rapid population growth when conditions are favorable. For example, arctic voles and lemmings reach reproductive maturity at 2 weeks of age.

The only porcupine found in far-northern environments is the North American porcupine. Two studies have described population cycles in North American porcupines: a study by D. A. Spencer in 1964 in Mesa Verde National Park in Colorado, and another by Klvana and coworkers in 2004 in Quebec, near the St. Lawrence estuary.

Spencer described population cycles over a 115-year time span (1840–1955), with four waves of porcupine abundance peaking in 1845, 1885, 1905, and 1935. Klvana and coworkers discussed six major waves over 125 years, peaking in 1875, 1900, 1925, 1945, 1965, and 1985. Both studies infer the population cycles indirectly, by counting and dating feeding scars, Spencer in piñon pine, Klvana in jack pine. Because feeding scars can be dated by a count of growth rings, one can deduce porcupine feeding intensity for the year in question. Neither study calibrates the relationship between feeding scars and porcupine density—that is, how many porcupines generate an observed density of feeding scars over the span of a population cycle.

There are reasons to think a constant conversion factor may not be applicable. For one thing, portions of the inferred cycles require a reproductive output of which the porcupine is not capable. Female porcupines begin to reproduce at the end of their second year of life and then produce a single porcupette a year. For competitive reasons, males don't become reproductively active until their fourth year of life. Yet Spencer shows his porcupine population increasing fivefold between 1876 and 1878, and by a factor of 4.5 between 1922 and 1925. Klvana and coworkers show a 24-fold increase between 1980 and 1988.

Another problem with ascribing a simple relationship between feeding scars and porcupine density is the diversity of porcupine diets. Porcupines at opposite sides of their species range may depend on entirely different

plant species. The same animal may also be feeding on a completely different species list in the winter than in the summer. What would happen if a pine forest were attacked by insects? Such infestations can be widespread and of long duration. As the trees struggled and declined, porcupines might switch to an alternate food supply. But the feeding-scar record would tally the switch as a population decline.

It is therefore important to calibrate the relationship between feeding scars and porcupine densities. Such work would not be easy. The Quebec cycles averaged 22 years. Biologists don't often undertake projects with a 50-year time spans. Until a long-term calibration is accomplished, the answer to whether porcupines undergo population cycles must remain a cautious "maybe."

Chapter 6

Reproduction and Development

How do porcupines reproduce?

The standard answer "very carefully!" is correct but not enlightening. An unwilling female can do as much damage to an aggressive male as she can to a predator within tail's reach. Because the female cannot be forced to copulate, the male must bring her to a state of willingness. This he does by urinating on her.

Precopulatory male urination is a part of North American porcupine courtship. The role of urine spraying in precopulatory behavior has not been studied in porcupines but has been studied in mice, where males use their urine more sparingly but no less effectively. A drop of male mouse urine brings a female into estrus (the stage where a female is receptive and can conceive). The phenomenon is known as the Whitten effect. The urine sprayed by a male porcupine is propelled at high velocity. This means that even if a male and female are sitting on separate branches in a tree, his urine can reach her.

Besides the urine foreplay, porcupine mating differs from human practice in that a female porcupine may mate only once a year. Matings are generally successful; well over 90% of adult females go through pregnancies and births every year. If the fertilization attempt is unsuccessful, the female's estrous cycle may resume, and she may make another attempt at mating a month later. (The estrous cycle in porcupines is the same length as in humans.)

Although the active partner during the urine-spray phase of mating is the male, the courtship has been initiated earlier by the female. North American porcupine females are solitary and live widely separated in the

forest. Dominant males shuttle between them. For a female to attract a male, she must signal to her suitors. As her period of estrus approaches, the membrane that had been covering her vagina weakens and disappears. The vagina begins to secrete a thick mucus which mixes with her urine and creates an odor plume as it drifts down the branches of her tree. Wandering males can follow the odor trail to the female.

When the male arrives, the female is usually not yet ready to mate. The male begins to guard her by sitting in her tree in a branch below hers. If additional males arrive, vicious battles may ensue until only the strongest, most determined male is left. Dominant males have large body weights, occupy large territories during mating season, and are typically at least 4 years old.

Although the victorious male has fought ferociously with other males, he must now use more gentle persuasion with the female. Urine spraying is his method, with just a few drops flying per salvo. Repeated salvos over many hours are required to bring the female into estrus and acceptance of the male. While the preliminaries have taken place high up in a tree, the copulation is typically accomplished on the ground.

Intromission follows the classic mammalian pattern: the female presents her raised hindquarters, tail curved back over the quills. The male penetrates while resting his paws on the quill-free tail undersurface or letting them hang loosely. After ejaculation, the male grooms himself, recovers, and may repeat the copulation many times until one or the other partner has had enough and climbs a tree.

Reproductive behavior in other New World porcupines awaits study.

Reproduction in the Old World Cape porcupine (*Hystrix africaeaustralis*) shows important differences between it and the North American species. While the North American porcupine males can mate with multiple females, Cape porcupines are monogamous. Since Cape porcupine males have no need to battle other males, they have not evolved body weights larger than those of females. (In fact, females are slightly heavier in this and other crested porcupine species.) Also unlike the North American porcupine, Cape porcupines mate multiple times throughout the year. After giving birth, the female experiences a series of "sterile" estrous cycles with matings but no pregnancies. The result is that the breeding pair averages one pregnancy a year.

The family group includes a breeding male and female, and typically two subadults (1–2 years old) and two juveniles. Fathers may mate incestuously with their subadult daughters, but such matings are sterile, with reproduction suppressed by the breeding female.

A male North American porcupine guarding a female on branch above, early October. Should a second male appear, the two will battle for right of access to the female.

Do porcupines always reproduce in the same season?

Among North American porcupines in New York State, 67% of all matings take place between mid-September and mid-October. For porcupines in the Great Basin Desert of Nevada, where spring comes later, the reproductive season also runs 2 weeks later. A New York porcupette conceived on October 1 would be born near May 1, the time of richest food supply, followed by months of mild weather and ideal growth conditions. Babies conceived after this date must crowd their all-important first summer of life into a shorter window of opportunity.

There is a more drawn-out reproductive season for the Old World Cape porcupine. Males and females are reproductively active throughout the year as the female cycles in and out of estrus. Nevertheless, 78% of litters are born in the rainy southern summer, the most hospitable time of the year.

By contrast, Roberts and co-workers have shown that in captivity, Brazilian porcupines (*Coendou prehensilis*) can reproduce at any time of the year. Estrus typically occurs 3 to 18 days after the previous birth. It is not known whether the young are born throughout the year under natural conditions. Tropical rainforests may show strong seasonal differences in rainfall and, farther from the equator, in temperature as well.

How is a male porcupine distinguished from a female?

Among North American porcupines, males are, on average, 20% heavier than females. But the range of weights is so large that a large female would easily dwarf a small-to-medium male. In Old World crested porcupines, it is the female that is the larger sex.

A key to male-female distinction in the North American porcupine is the tuft of white quills on top of the head. The tuft is typically more luxuriant in males than females, irrespective of the weight of the animals. The white head tuft is likewise a variable character. It is more prominent in individuals from the eastern part of the species range than in those from the west.

A more accurate method is to turn the animal over and examine the genital region. Both males and females show an anterior urethral opening (the penis is not externally visible). Between the urethra and anus, and lateral to the midline, lies a pair of perineal glands. In males, the openings of the glands lie as slits perpendicular to the midline. In female, the openings lie parallel to the midline. In adult males, a pair of plump swellings is visible under the skin, lateral to the urethra. These are the testes in their descended position. Typically, the testes are visible only in late summer and fall.

The best and most definitive method of sex determination is to pinch down lateral to the urethra. If the animal is a male, a penis will evert. If it is a female, the urethral opening will only spread more widely. It goes without saying that the technique should be attempted only with immobilized porcupines. A similar technique of attempted penis eversion will work with other New World and Old World porcupines. In all porcupines, the vagina is normally closed by a vaginal closure membrane, and the penis is retracted.

How long are porcupines pregnant?

Porcupines, especially in the New World, have relatively long pregnancies for mammals. A North American porcupine (*Erethizon dorsatum*), with 10% of the body weight of a human female, has a pregnancy almost as long: 7 months. Its South American cousin *Coendou prehensilis* comes close with a 6.7-month (202-day) gestation period. By contrast, the Old World Cape porcupine (*Hystrix africaeaustralis*), though heavier, has a pregnancy less than half as long: 94 days.

The shorter pregnancy of *Hystrix* follows from the smaller ratio of birth weight to maternal weight in this species. In *Hystrix*, litter weight represents only 3% of maternal weight (assuming average litter size of 1.5). In

Birth weights and gestation lengths in three porcupine species

Species	Maternal wt. (kg)	Neonate wt. (kg)	Gestation (days)	Birth wt. (%)
Erethizon dorsatum (N. America)	4.6	0.45	210	9.8
Coendou prehensilis (S. America)	4.0	0.42	202	9.5
Hystrix africaeaustralis (Africa)	18.4	0.35	94	2.9[a]

[a] Assuming an average litter size of 1.5.

both *Erethizon* and *Coendou*, the newborn weight represents about 10% of maternal weight. Though Cape porcupine babies are born with eyes open, quills in place, and some teeth erupted, their immaturity is shown by the fact that they spend the first 9 weeks of life inside their burrow. By contrast, newborn *Erethizon* and *Coendou* are moving about from the first day. The long gestation periods of the New World porcupines can therefore be thought of as a form of extended maternal care.

How is a baby porcupine born?

In the North American porcupine, as a female's vaginal closure membrane begins to dissolve, she prepares to give birth. She chooses a birth site where the baby can be well hidden. For the first two weeks of life it will be unable to climb a tree, nor will it be strong enough to offer an effective quill defense. A favorite birthing site is an area covered with broken trees such as left by lumbering operations or windstorms. Here the baby is hidden in the dark shadows under broken trees. Also favored are shallow rock crevices with entrances obstructed by tree slash.

The porcupette is born like a cat, wrapped in its amniotic sac, or caul. The fetal membrane protects the birth canal during delivery. After birth, the mother licks away and consumes the caul, recovering its valuable nutrients and minerals. Because the baby is born in its caul, the mother must deliver a higher birth weight. At birth, a North American porcupette weighs about 10% of its mother's weight. But because of the added weight of the caul, its effective birth weight might be 12% to 14% of the mother's weight. Fortunately for porcupines, the pelvic girdle is wide enough to provide a comfortable passage, and porcupine mothers are not incapacitated following birth.

How many babies do porcupines have?

North American porcupines in the wild bear no more than one baby a year. All births occur in the spring, and twin births have never been ob-

A newborn North American porcupette. The erected quills of the back, normally hidden under thick black fur, are only 0.2 inch long and useless for meaningful defense. Its insecurity is compounded by the fact that it cannot yet climb a tree.

served. Brazilian porcupines also give birth to a single young, but females go into estrus 3 to 18 days after giving birth. Since these porcupines have a gestation period of 202 days, about 1.5 offspring can be delivered per year. Brazilian porcupines can breed continually because they live in a tropical climate.

Cape porcupines typically have one litter a year, delivered in the rainy southern summer. Litter size is variable, with 59% singletons, 32% twins, and 9% triplets, for an average of 1.5 offspring. The young have very high survival probabilities.

What is a baby porcupine called?

A baby porcupine is called a porcupette. Since the name has a feminine ending, it can be used for babies known to be female or babies with sex undetermined. If a baby is known to be a male, it is called a porcupet.

The terms *porcupette* and *porcupet* are specific to the porcupine, as *cygnet* is to the swan, *kitten* to the cat, *fawn* to the deer, *foal* to the horse. Some biologists have referred to baby porcupines as pups. This is a less specific and therefore less desirable term. Pups can be the offspring of dogs, rats, mice, seals, otters, foxes, even sharks. Why join the porcupine to this long list?

Do porcupines care for their young?

In the North American porcupine, the father provides no care for his infant offspring and does not live with the family group. Maternal care takes the form of extended pregnancy and nursing; porcupine mothers nurse their babies once a night. For the first 2 weeks of its life, this is the

only food the porcupette receives. The mother also removes the newborn's droppings, removing an odor cue that could attract predators.

After two weeks, the baby learns to climb increasingly larger trees and supplements its mother's milk with green vegetation. During the first few weeks of life, the baby stays within close proximity to the mother, although the baby initially remains on the ground with the mother up a tree. Later in the summer, the two may forage in different parts of the forest, with the mother sometimes traveling long distances to reach her baby for the nightly nursing. The porcupette continues nursing for 4 months, until the beginning of the fall mating season.

The summer-long nursing represents a significant metabolic cost to the mother. A study in Quebec by Berteaux, Klvana, and Trudeau found that nonlactating females added 65% body weight from May 1 to October 20 while lactating mothers added only 40%.

Maternal care does not extend to physical defense of the young when a human researcher tries to capture it. Even when I have captured a baby in view of the mother and the baby was struggling, the mother did not move to defend it. This may be a response to past experience. All the mothers with whom I interacted were wearing radio collars and had experienced their own powerlessness before. In addition, they may have concluded that I was not a threat to them or their babies. The mothers' lack of response in these situations does not indicate callousness or lack of concern. When a porcupet I had radio-tagged fell to his death out of a bigtooth aspen where he had been feeding with his mother, the mother descended and waited next to her young son's body for hours, waiting for him to revive. The baby had died instantly of a broken neck.

Here, a one-week-old North American porcupette is hidden under the root mass of the central tree, its quills barely visible. Its mother is in the branches of the tree above. Because the baby is still too young to travel or climb trees, the mother remains in close proximity, descending to the ground regularly to nurse.

A female Brazilian porcupine observed by Roberts and coworkers at the National Zoo in Washington, D.C., nursed her infant almost as long as female North American porcupines do (15 weeks), with several feedings per day. The baby was totally dependent on mother's milk for 4 weeks. Neither parent defended the infant or herded it away from danger. In a zoo setting, with both parents and offspring present, the baby enjoyed long periods of play, either alone or with the parents, and especially with the father. Neither parent lost patience with the baby or became aggressive towards it.

Old World Cape porcupines and other *Hystrix* porcupines have a monogamous mating system, a social system found in only 3% of all mammals. The animals live in family groups that include undispersed subadults and juveniles. Family groups (which may include up to 14 members) share a burrow. An important part of parental care in such burrow living is the energy conservation resulting from huddling. Newborns remain huddled in the burrow for the first 9 weeks of life. During this time, the burrow offers the added advantage of protection from predators, with 100% of newborns living to 2 months, and high survival afterwards. Nursing lasts for 110 days, almost as long as in New World porcupines.

Unlike the males of New World porcupines, Cape porcupine males provide parental care by huddling in the burrow, grooming their offspring, and accompanying the young on foraging trips outside. There, they will actively defend their young from predators.

Similar mating systems and patterns of parental care are shown by Old World brush-tailed porcupines. While newborn Asiatic brush-tailed porcupines (*Atherurus macrourus*) are active and well developed, they require long periods of nursing. Both parents guard the young, accompanying them on their first excursions outside the maternity chamber.

How long do female porcupines nurse their young?

In the North American porcupine nursing lasts an amazing, by rodent standards, 4 months. Therefore, a female who has completed a 7-month pregnancy is spending 11 months out of 12 either pregnant or lactating, with no years off for recovery. It is this huge maternal investment that virtually ensures that the baby porcupine will survive its first summer and fall.

In the Brazilian porcupine, *Coendou prehensilis*, lactation lasts 3.7 months (15 weeks). For the first 4 of those weeks, the mother's milk represents the baby's sole food supply. A *Coendou* female can start her next pregnancy while still nursing. By contrast, an *Erethizon* mother conceiving in May would deliver her baby in December snows.

In the Old World Cape porcupine (*Hystrix africaeaustralis*), lactation lasts 101 days (14.4 weeks), and nursing does not overlap with the subse-

quent pregnancy. Though *Hystrix* porcupettes are less developed at birth than those of *Erethizon* or *Coendou*, they receive sufficient parental care to allow all offspring to survive to the age of 2 months. Survival to age 12 months ranges from 84% in high-density populations to 100% in low-density populations.

How fast do porcupines grow?

Among New World porcupines, North American porcupines show the most explosive growth: they double their birth weight in 2 weeks. Fortunately, this rate of growth slows, so that by the end of their first summer of life, they exceed their birth weights by only 4 to 6 times, not the 256 times that would have occurred had the pace of the first 2 weeks been continued. By comparison, the Brazilian porcupine (*Coendou prehensilis*) takes over a month to double its birth weight of just under a pound (0.42 kg).

North American porcupines live in a temperate climate, with brief, food-rich summers and long winters of starvation. As a result, weight gain in *Erethizon* is stepwise: weight increases in spring and summer, and decreases in winter. The animal that does not enter winter with adequate energy reserves, as expressed in body weight, does not survive. The *Coendou* faces no similar challenges. *Erethizon* does not reach its adult weight of 10 to 11 pounds (4.5–5 kg) until the end of its second summer, at about 16 months of age.

In Cape porcupines, birth weights average three-quarters of a pound (350 g). Animals reach the adult weight of 26 pounds (11.7 kg) in 42 weeks. This corresponds to a 33-fold gain in body weight.

How can you tell the age of a porcupine?

The age of a North American porcupine can be determined reliably during its first two years of life by a dental examination. The baby is born with 8 teeth: 2 upper and 2 lower incisors, and 4 deciduous premolars, one in each quadrant of the jaw. During its first summer, it adds 2 molars to each quadrant, for an additional 8 teeth. At the end of its first year of life (the beginning of its second summer) it adds a third molar to each quadrant. It now has the full adult number of teeth (20) but not yet the adult complement. That is reached at age 2, at the beginning of its third summer, when the deciduous premolars are replaced with adult premolars. Adult premolars in North American porcupines are noticeably larger than either the molars or the old deciduous premolars, and are easily identified. Beyond age 2, the tooth complement does not change.

To determine the age of animals older than 2, Earle and Kramm ex-

Two-month-old North American porcupine in an apple tree. Long fur and guard hairs conceal its quills. At this stage, the porcupette is able to climb as well as its mother and travel with her through the forest. Its most important task is to put on sufficient weight to survive its first winter alone.

tracted a molar or premolar, decalcified the tooth with mild acid, then cross-sectioned and stained it. Each year of life shows up as a growth ring in the root of the tooth. Thus, an 8-year old porcupine would show eight growth rings in the first or second molars, seven in the third molars, and six in the premolars. The method has not been tested in porcupines from regions outside North America.

When porcupines reach ages above 20, their molars begin to show noticeable wear of grinding surfaces. Such wear is visible by external examination; no sectioning is necessary. One would expect to see similar age-related changes in all porcupine species, since no porcupine has ever-growing molars. Old World crested porcupines, who dig for their foods, face increased wear because of the grinding action of soil particles attached to their food. In compensation, their molars are high-crowned, extending unusually far above the gum line and providing additional tooth material for wear. Cows, horses, and deer also have high-crowned molars.

Other physical changes of extreme old age (25+ years) include whitening of the fur of the muzzle and the face and a possible variety of skeletal pathologies: arthritic lesions of hip and shoulder joints, fusion of wrist or ankle bones. Because female North American porcupines may undergo menopause (they cease reproductive cycling years before death), it is possible that their bones become thinner and more brittle as a consequence of the shutdown of estrogen production, but this question has not been experimentally investigated.

At what age do porcupines start breeding?

Females of the North American porcupine start breeding at the end of their second summer of life (at the age of about 17 months). Very rarely, a female may breed at the end of her first summer. Males become able to breed at age 2, when their testes descend; but to get access to females, they must be able to compete with older, more dominant males. This does not happen until about 4 years of age, when maximal body weight has been reached. In some males, the process may take longer. How long a dominant male holds its position is not known. The long delay to breeding status, and the small reproductive output (one offspring per female per year) make for a slow growth rate in North American porcupine populations.

Brazilian porcupines substantially follow the *Erethizon* pattern. For females, the age at sexual maturity is approximately 19 months. Nothing is known about male competition in the wild. But because the interbirth interval is shorter in *Coendou*, their populations can grow faster than those of their northern cousins.

In Old World Cape porcupines, a female reaches sexual maturity during her second year of life, when she may mate incestuously with her father. However, the matings are sterile until she disperses out of her natal den. Sexual maturity for a male comes between 8 and 18 months of age, but to produce offspring he must first leave the natal den and establish a family with a willing female.

Do female porcupines go through menopause?

Menopause (literally, the cessation of menses) is defined as the permanent end of ovulation and fertility. In humans, the ovulatory cycles become irregular before stopping completely, and levels of the ovarian hormones estrogen and progesterone fall drastically.

Female North American porcupines may also go through menopause, as documented in a single wild female I followed by radiotelemetry for most of the 21 years of her life. During this period, with few exceptions, she became a mother every spring. But for the last 4 years of her life, she stopped participating in the fall mating season and bore no offspring the following spring.

Biological conclusions based on a single case study raise the question of whether the observations can be repeated. Fortunately, there is a pool of animals where 21-year studies may not be required: zoo porcupines. Typically, accurate age records are kept for zoo porcupines, and keepers or veterinarians are able to assess the animals' reproductive status. It is hoped that such studies will be carried out, and in more than one species of porcupine.

The onset of menopause in my old female was signaled at age 17, when she first failed to participate in fall mating. A female normally takes part in the mating process because her ovarian hormones are surging, causing physical changes in the vagina and sending olfactory signals to males. I trapped the female in winter snow 4 months after the mating season had ended and was surprised to find the vaginal closure membrane open and ready for mating. But with winter snow on the ground, all males were in their dens and unavailable. Thus, in porcupines as in humans, the onset of menopause is signaled by irregularity of the ovarian cycles. In my porcupine female, I found no evidence of cycling in subsequent years.

Unexpectedly, her body condition improved after menopause. For the 3 years preceding, her average summer weight had been 14.5 pounds (6.6 kg). In the following 3 years, freed of the drains of pregnancy and lactation, her average weight rose to 16.3 pounds (7.4 kg). Adequate body weight is an insurance policy for surviving the harsh northern winters.

In humans, the biological advantage of menopause has been explained in terms of the grandmother effect: a woman of advanced years can achieve greater reproductive success by caring for grandchildren than by bearing more children of her own late in life. The grandmother effect cannot explain the evolution of menopause in porcupines because porcupine females do not know their own grandchildren (their daughters disperse as juveniles), and they could not provide meaningful care even if they knew them.

Shripad Tuljapurkar and colleagues have suggested an alternate explanation for the evolution of menopause in animals like porcupines. They propose that menopause evolves as a consequence of May-September mating systems. In primitive human societies, there is typically a 10 to15 year difference in ages of the bride and groom. Young women choose older men because they command greater resources; older men choose younger women because they are more fertile. In such May-September marriages, the fathers contribute longevity genes to all their offspring, male and female alike. Such longevity genes in females can extend their life span beyond the functional age of the ovaries.

Do porcupine matings typically match older males with younger females? Though much field study remains to be done, this appears to be the case. Porcupine females begin mating at the end of their second summer of life. Porcupine males must battle their way to the top of their reproductive hierarchies. Work by Sweitzer and Berger in the Nevada desert shows this happens around age 4. I have trapped marked 4-year-old males in the Catskills who were clearly still shy of dominance status. They may reach that milepost by age 5, or 6, by which time their mating relationships will predominantly be May-September.

Earle and Kramm have determined the age structure of a population of 20 porcupines from Michigan's upper peninsula. The median age—the age at which half the population is younger, half older—was 2 years. The average age was 4.2 because the population included two older females aged 14 and 15, respectively. Hence a 4-year old male in this population would find most of his mating partners significantly younger than himself.

Of course, a 15-year-old female might reverse this relationship by mating with a younger dominant male, but such females would make up a small fraction of the breeding population.

How long do porcupines live?

A North American porcupine who carried a radio collar and an identifying tattoo lived for 21 years in the wild. At death, she displayed only subtle signs of aging: the fur on her muzzle showed the beginnings of whitening, and on one molar, the enamel grinding ridges had been worn down close to the pulp. Another female, captured in the wild and released after examination, was an estimated 25 to 30 years old. Her muzzle was entirely white, while the rest of her fur retained its black color. All her cheek teeth had been worn smooth. She was smaller than the 21-year-old female.

M. L. Jones has collected longevity data for zoo animals. He notes a captive South American *Coendou prehensilis* that lived for 17 years, 4 months. Crested porcupines of the Old World live to 21 years in captivity (though animals in the wild average only 10 years). A captive Himalayan porcupine, *Hystrix brachyura*, who lived for 27 years, 3 months, holds the longevity record for porcupines. A captive African brush-tailed porcupine, *Atherurus africanus*, lived 22 years and 11 months in captivity. A captive long-tailed porcupine, *Trichys fasciculata*, was still living at age 10 years.

Both New World and Old World porcupines have longer life expectancies than might be expected on the basis of their body size. (Large body size correlates with long life expectancy.) It should be remembered, however, that the numbers provided above represent observed maxima, not averages. A porcupine population with high mortality from severe hunting or predator pressures will have little chance of achieving these maxima.

What sets the upper limit to porcupine life expectancy? Even in the absence of predator pressure, an upper limit appears to be set by tooth wear. Once a porcupine wears out its grinding teeth, its feeding is compromised, and it starves. Though porcupine incisors are ever-growing and continually replaced despite heavy wear, the same is not true of the cheek teeth. In very old animals, the premolars and molars are worn so heavily the teeth lose their grinding surfaces and become worn down to the gum line.

How do individual porcupines differ in reproductive success?

The reproductive success of an animal is defined as the number of offspring it produces over a defined time span. For meaningful discussion, that time span should be the animal's lifetime. Reproductive success can be thought of as the driving force of evolution. Only the organisms that successfully reproduce can leave their imprint on future gene pools. Because of the link between reproductive success and the gene pool, biologists usually define reproductive success as the number of offspring produced that survive to reproduce themselves. These data are not available for any porcupine species; thus, the less restrictive definition will be followed here.

In a study of reproductive success, many questions can be asked. For instance:

- How much variation is there between individuals of a population? As an example, it has been estimated that Genghis Khan has left 16 million descendants. This would make him 800,000 times more successful than the average man of his age.
- Which sex shows greater variation?
- What components of reproductive success contribute most to the variation? T. H. Clutton-Brock of Cambridge University suggests some possibilities: longevity, fecundity, mating success, offspring survival.

In North American porcupines, the only porcupine species in which reproductive success has been studied, females begin breeding at age 1.5, males at age 4 or later, according to my studies in New York and those of Sweitzer in Nevada. Lifetime reproductive success has been studied in only a single animal, a New York female who was radio-collared from age 1 until her death at age 21. At age 17, she entered menopause and stopped breeding for the last 4 years of her life. During her lifetime, she gave birth to 13 offspring. It is impossible to generalize from a single case study. The female was the longest-living porcupine in the New York study and was clearly exceptional; most females died or dropped out of the study at much younger ages.

No comparable figure is available for any male. In males, breeding success must be estimated indirectly, from the number of observed annual guarding episodes. A genetic study, which would give a more comprehensive answer, has not been carried out for any porcupine species.

Without such lifetime data, the New York and Nevada studies offer cross-sectional information collected from different sets of individuals and different time periods. Thus, the New York study followed six males through the 1987 breeding season. The average mating success was 1.17,

but the range of variation was high, from 3 for two males to 0 for three others. For three New York females followed over 6 years, the average reproductive success was 0.94 per year, with very little variation. Almost every female produced a single offspring every year.

In the Nevada study, the average mating success for males was 1.80 (again extrapolated from observed guarding episodes), with success rates varying from 0 to 3 per animal. The female success rate was 0.91, with little variation between animals.

The initial conclusion is that males show much higher variability in reproductive success than females. This is apparent in both studies, which show males as the variable sex, with females equal and nearly invariant, since almost all adult females produce one porcupette per year.

But would the males show such high variability if followed over a lifetime? The variability in male mating success comes from the fact that the New York data set includes juveniles and young adults who have not yet reached adult weight and have little competitive edge. (The Nevada data set excludes juveniles.) How would the younger animals perform if examined 2 or 3 years later? It is possible that all males start life undersized and reproductively excluded, then become successful during their peak years, declining once more in old age. Only a study across a lifetime could prove or disprove the hypothesis.

What if a male reaches peak reproductive condition but is nevertheless shut out by a more powerful male? There is a suggestion that such unsuccessful males may leave their home ranges and disperse to distant lands where better luck may await. This was the path chosen by one large but unsuccessful male in the New York study. The animal left the home range where he had been born and reached maturity, and began to travel northwest. He moved slowly, well below his physical capacity, as though testing his new environment. On reaching the outskirts of a small town, he disappeared, most likely the victim of a local property owner. His abandonment of the territory of his birth had ended in death.

Chapter 7

Foods and Feeding

What do porcupines eat?

The North American porcupine, like all other porcupines of the world, is a herbivore. It consumes plant foods, mostly tree leaves and bark, as well as seasonal fruits and mast. Though it encounters birds' nests with eggs and nestlings, it is not known to prey on them as a squirrel or chipmunk might. Porcupines are sensitive to seasonal changes in their forest foods and respond by changing their diets as food options change. They are also highly selective in their feeding choices. For instance, porcupines feed on the buds of sugar maples as these swell in the spring, ignoring the twigs on which the buds are located, and ignoring as well buds that have opened (such buds show sharply elevated tannin levels). Later in spring, they feed on the young leaves of beech and ash, selecting only the leaf blades, not the petioles (leaf stalks).

In terms of food chemistry, porcupines prefer foods with high levels of protein and avoid foods with high levels of plant defense compounds such as tannins and phenolic glycosides. These twin constraints narrow the species base of the porcupine's summer foods. In eastern mixed coniferous forests, 90% of the summer diet consists of the leaves of linden (*Tilia americana*) and aspens (*Populus tremuloides*, *P. grandidentata*). Porcupines may supplement their tree-leaf diets with ground-level foliage, such as the leaves of blackberry and raspberry.

In late summer and fall, North American porcupines seek out fruits (mountain ash, apple) and mast crops (beechnuts, acorns), which they consume while the fruits and mast are still up in the trees.

There is one missing element in all of the porcupine nonwinter foods:

Porcupine feeding in apple tree. The long claws of the animal can be flexed to hold the apple against the footpad.

sodium, most commonly obtained as salt. Plant foods are overly rich in potassium, which must be excreted in the urine to preserve the 1:1 potassium-sodium ratio that body cells of animals must maintain for proper nerve and muscle function. Porcupines often seek their sodium supplements from human sources: road salt, plywood resin, rubber tires, sweat-soaked tool handles. These activities are the most common cause of human-porcupine conflict. Porcupines may also exploit natural sodium sources such as the leaves of yellow water lily, arrowhead, and aquatic liverworts. And they have been known to gnaw on the bones of fresh carrion, which contain significant levels of sodium.

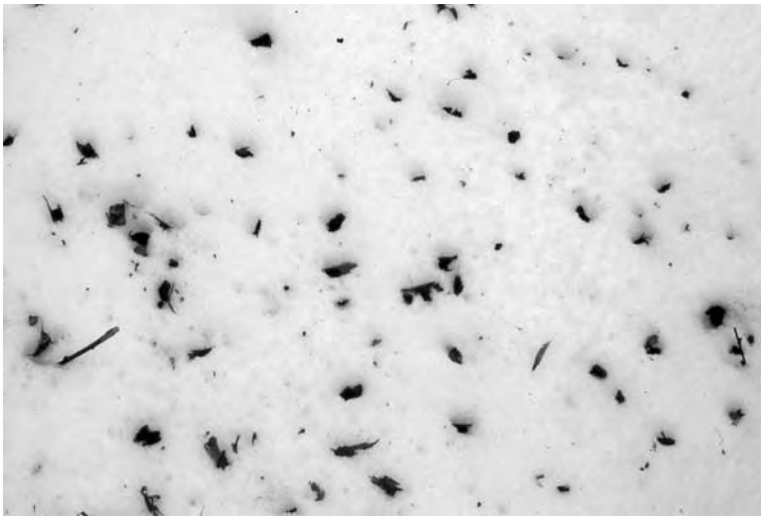
During the winter North American porcupines feed on the living inner layers of tree bark. In hemlock, an important winter food, the animals eat needles and twig tips, which contain lower tannin levels than does the bark. They also eat the bark of a wide variety of tree species: maples, beech, linden, pines, and spruces, to name a few. Such feeding leaves a conspicuous signature on tree bark, and extensive feeding can deform or kill a tree. Fortunately, most winter feeding is restricted to small patches of forest surrounding the winter dens. A diet of tree bark is low in nutrients and high in fiber and plant defense compounds. Consequently, all North American porcupines lose weight during the winter.

South American porcupines are not confronted with the winter loss of tree leaves and fruit and therefore do not have to resort to bark feeding. A

Winter bark feeding by the North American porcupine. During feeding, the animal holds its place with the upper incisors while swiveling its jaw and scraping with the lower incisors to produce a tepee-like pattern.

The North American porcupine processes hemlock differently than it does its other winter foods. Because hemlock bark contains very high tannin levels, the porcupine feeds on terminal twigs instead, cutting them near the tip and then consuming the needles.

study by de Souto Lima, Oliveira, and Chiarello shows that *Chaetomys subspinosus*, the thin-spined porcupine of southeastern Brazil, eats the leaves of a small number of tree species. The most important of these is *Pera glabrata*, a member of the spurge family that is related to the Brazilian rubber tree. The porcupine feeds selectively. Once anchored in the tree by means of its tail and hind limbs, it uses its forelimbs to grasp thin, leafy branches and pull them in front of its face. It sniffs the leaves, apparently to verify their edibility, then chews and swallows. In many instances, the porcupine consumes only the leaf blades, leaving the petioles on the branch. In its avoidance of petioles, it mimics the North American porcupine.



Bark chips in the snow. When the North American porcupine feeds on thick bark, it discards the dead outer layer, then makes a second pass with the incisors to harvest the inner, living bark. To minimize their feeding effort, the porcupines generally feed on the upper branches in the canopy, where the bark is thin enough to be harvested in a single pass.

The study by de Souto Lima and coworkers was carried out in a forest type called the Restinga. The canopy is low and threaded with vines and lianas. There is a rich diversity of tree species despite the sandy or nutrient-depleted soils. A more extensive study of the thin-spined porcupine's feeding biology was carried out by Gine and coworkers, 470 miles (750 km) to the north, in a forest with a higher canopy and more complex vegetation. This portion of the Atlantic Forest harbors the largest known contiguous population of the thin-spined porcupine. Like the more southerly porcupines that de Souto Lima and associates studied, these porcupines fed exclusively on tree leaves and showed great selectivity of feeding choice. Over 86% of their feeding was focused on just three tree species: the *Pera glabrata* observed by de Souto Lima and associates, plus two leguminous trees, *Albizia pedicellaris* and *Inga thibaudiana*. These three species make up just 7% of the surrounding forest.

Gine and coworkers observed that the three tree species in the porcupine diet are all pioneer species: they require open sunlight or forest openings for establishment. Pioneer species can grow rapidly in open sunlight because they don't invest heavily in plant defense compounds; this makes them attractive to mammalian herbivores. The pioneers are replaced by slower-growing, highly defended climax species as the forest ages. Because the Atlantic Forest of Brazil is fragmented and under severe development pressure, pioneer tree species find many opportunities for establishment and growth. So many food trees are available that the porcupines can survive on relatively small home ranges of 4.7 acres (2.14 ha) per animal, according to a study by Oliveira and coworkers.

Besides selecting pioneer tree species, the thin-spined porcupines selected young leaves to feed on. Young leaves typically have higher pro-

tein and lower fiber (indigestible carbohydrate) levels than do mature leaves.

Another porcupine from Brazil, the Paraguayan porcupine (*Coendou spinosus*), feeds exclusively on young leaves from six tree species, as reported by Marcelo Passamani. (In Passamani's nomenclature, the animal is *Sphiggurus villosus*.) Like the thin-spined porcupine, it is a dedicated leaf-feeder.

Whereas the thin-spined and the Paraguayan porcupines are small porcupines, the Brazilian porcupine, *Coendou prehensilis*, is the largest in South America. In a study of this porcupine Charles-Dominique and coworkers observed the animals feeding on the unripe fruits of a variety of tree species. The animals are so effective in their harvest that some biologists believe they could be partly responsible for the evolution of mass flowering in these trees. By synchronous fruiting, trees can satiate their seed predators.

Old World long-tailed porcupines (*Trichys fasciculata*) have broad diets that include foods obtained both on the ground (primarily fallen fruit) and in trees and shrubs: leaves, fruits, growing shoots, bark, and occasional insects and small invertebrates. Miura and coworkers set up a camera trap in a Malaysian tropical forest to record consumption of fallen fruit. A selection of forest fruit was placed under a tree, with an infrared trigger activating a flash camera. The authors recorded 35 animal species taking the fruit. In 2,738 successful photos, the long-tailed porcupine was the second most frequently observed visitor (579 photos). Also observed was the Himalayan, or Malayan, porcupine (*Hystrix brachyura*), caught in 107 photos. The Asiatic brush-tailed porcupine was not present in the local forest.

Old World brush-tailed porcupines depend heavily on fallen fruit for food. However, they also dig for underground plant parts. Old World crested porcupines (*Hystrix africaeaustralis*, *H. indica*, and *H. cristata*) dig for bulbs, roots, and tubers. During the dry season, they also feed on inner tree bark to a height of 0.5 m up the tree trunk, which they can reach without climbing.

How do porcupines find food?

For a North American porcupine, the foods sought through most of the year are leaves and fruit high up in forest trees. These are items that are hard to see from the ground even in daylight, and a porcupine feeds mostly at night. Yet porcupines don't climb trees by trial and error until they find the right species. They identify trees by the only signal available at night, their smell.

Climbing the correct species isn't always enough. Linden and quaking aspen are two preferred food species of summer and fall. Yet to a porcu-

A Brazilian porcupine feeding on a leguminous fruit—a peanut—in the Bronx Zoo. In the wild, the porcupine feeds in the tree canopy and favors immature fruit.

pine, not all linden and aspen leaves are alike. Some trees are heavily used, while others, in close proximity, may be ignored. How does the animal identify the preferred trees? It marks them with its urine. The urine mark may be as slight as a few drops at the base of the tree, or it may be a whole shower released from the canopy. The urine marks are surprisingly persistent and can be detected by a porcupine for at least a week afterward, even following heavy rain.

Old World Cape porcupines (*Hystrix africaeaustralis*)—which feed on underground bulbs, corms, and tubers—also mark their feeding sites, as shown by the work of de Villiers with leash-walked porcupines. They mark by a process of anal dragging, which deposits the secretions of the perineal glands located between urethra and anus.

Philip Alkon, in a study of Indian crested porcupines (*Hystrix indica*) in the Negev Desert of Israel, equipped the porcupines with acoustic transmitters, which sent back information about the animals' audio environments. He found that on foraging expeditions, a common activity was heavy sniffing. Alkon believes this was associated with food search. The porcupines were able to identify the precise locations of subterranean bulbs, roots, and tubers before starting to dig.

Do porcupines scavenge?

Scavengers are carnivores that feed on a carcass they did not kill themselves—a jackal at a lion kill, a crow at a car kill. If for no other reason

than their herbivore status, porcupines are not a part of such assemblies. However, in specific circumstances, porcupines can take on some of the attributes of scavengers.

The tree leaf diet of the North American porcupine is deficient in one essential nutrient: sodium. Porcupines must therefore seek sodium from other sources, often ones associated with humans, but porcupines can also feed on a natural sodium source: the leg bones of a recent deer kill. Fresh bone is a good sodium source, containing about 25% of the deer's total sodium. The calcium of bones is not attractive to the porcupines, whose leaf diet is so calcium-rich that the ion must be excreted in the urine.

It is possible for porcupines to feed on other parts of carrion as well, but bones are usually all that is left after other scavengers finish with a carcass. Trappers report frequent captures of porcupines in traps baited with "ripe" meat and set for other animals.

Old World Cape porcupines engage in scavenging of a different sort: they collect bones and carry them to their burrows, where some bones are gnawed and others left to accumulate. For example, C. K. Brain describes a cave in the Kalahari Desert that yielded 1,708 bones, of which 60% were gnawed. The origins of the bones closely reflected local population densities of animals such as springbok, gemsbok, hartebeest, and wildebeest.

Unlike the North American porcupine, the Cape porcupine selects bones that have been whitened and cracked by long exposure in the sun. Two theories have been offered for the basis of the bone collecting. The bones may be used to sharpen the porcupine's ever-growing incisors. Or the bones may represent a source of phosphate for the porcupine. Bone chewing is more prevalent in phosphate-depleted regions.

In addition to bone chewing, Cape porcupines may also occasionally feed on classic carrion.

Do porcupines store food?

In a manner of speaking. The North American porcupine stores food, not as a squirrel or chipmunk might, by depositing mast in a hidden location, but by storing the food in its own body, as fat deposits.

North American porcupines undergo large fluctuations in body weight through the course of the year. In late summer and fall, they feed on leaves and available mast (acorns, beechnuts) and reach their peak body weight. The bulk of the added weight is deployed as a thick layer of fat under the lower back, where it serves the double function of food reserve and insulation.

Berteaux and coworkers found that nonreproductive females in Quebec

added 65% to their spring body weights by the end of fall. Gains of about 40% were observed in lactating females and adult males, who spent energy in reproductive processes. These body stores were depleted over the course of the winter, as would be the acorns or beechnuts stored by a squirrel or chipmunk. Both Richard Sweitzer and I have obtained similar data.

Why do porcupines eat clay?

I have recently observed that North American porcupines regularly consume clay. This behavior has long been known in a wide range of other mammals and birds—elephants, bats, livestock, deer, giraffe, rabbits, primates, parrots, macaws.

There are two leading hypotheses to explain clay-feeding (geophagy) in animals. One sees it as a form of sodium (as salt) acquisition. There is little doubt that sodium seeking explains the behavior of African elephants. They engage in geophagy only when living in sodium-depleted environments. Holdo and coworkers have shown that soils consumed by elephants have elevated sodium content, and that the intensity of geophagy in these animals rises as body sodium levels fall. The studies of Brightsmith and Munoz-Najar in Peru suggest that sodium seeking may also explain the clay feeding of Peruvian macaws.

The alternate, competing hypothesis sees geophagy as a defense tactic against plant toxins. All the soil-feeding animals listed above are herbivores. Since plants can't run from their herbivore predators, they typically defend themselves chemically. Tissues of wild plants can contain a potent mix of poisons that can sicken or kill. (Humans have bred the toxins out of most cultivated grains and vegetables.) If a herbivore is specialized in its diet, as are many insects, it can evolve metabolic countermeasures to specific plant toxins. But mammals have broad diets; and their detoxification mechanisms are by necessity broad based, only partly effective, and metabolically expensive.

For most mammals, the heavy work of detoxification takes place in the liver. This is why the venous blood leaving the small intestine, and carrying potentially toxic molecules absorbed from the food, does not directly join the venous return to the heart. It moves first to the liver via the hepatic portal vein. There, the vein breaks up into capillaries and the blood is exposed to liver enzymes called oxidases. Oxidases add oxygen groups to potentially toxic molecules, making them both less toxic and more easily excreted by the kidneys.

In the kidneys, the oxidized toxins are linked to water-soluble carriers, such as modified sugars, and excreted in the urine. The excreted sugar

derivatives represent a significant energy loss. Coltrane and Barboza have shown that free-ranging Alaska porcupines lose 21% of their dietary energy intake in the urine. This drain is responsible for the winter weight loss of the animals. Porcupines fed an artificial diet with energy, nitrogen, and fiber content similar to that of the natural diet but lacking the plant defense compounds were able to maintain normal body weight throughout winter.

Another detoxification mechanism used by many herbivores is the secretion of proline-rich proteins (PRPs) in the saliva. The PRPs form complexes with dietary tannins released from chewed plant foods and escort them through the intestines without absorption into the blood stream.

Clay ingestion represents a substitute detoxification strategy. Gilardi and coworkers have demonstrated that clays can complex tannins, a major class of plant defense compounds. They can also adsorb a variety of toxic alkaloids. And as an added bonus, clays work with no metabolic cost to the ingesting animal.

The detoxifying properties of clays have not been lost on the health care industry. Kaopectate, an antidiarrheal medication approved by the FDA, contains kaolin as its active agent. Kaolin is an aluminum silicate clay that complexes the diarrheal bacteria and their toxins.

To evaluate the two competing theories with respect to porcupine geophagy, I conducted a study in the Catskill Mountains of New York to measure both salt drive and geophagy in the local porcupine population as a function of season. The two processes had different seasonal courses. The porcupines' salt drive peaked in May, but geophagy increased from spring to fall, peaking in October. Sodium seeking therefore cannot be the only explanation of geophagy in the North American porcupine.

How often do porcupines drink?

Captive North American porcupines need to drink regularly, but the diet of captive porcupines is dry rodent chow or other dry foods, supplemented with fruits or vegetables. The dry foods contain no liquid and contain salts which need water for kidney clearance.

The situation is different in porcupines' natural environment. Their normal diet of tree leaves contains sufficient water to satisfy normal metabolic needs. To confirm that this is true, I maintained porcupines for 5-day periods on a diet of fresh tree leaves, with no supplemental water offered. The animals showed no weight loss or lethargy and had no interest in water offered at the end of the experiment. Thus, free-living North American porcupines do not travel to water sources to drink, as do white-tailed deer or carnivores.

Gine and coworkers report a similar behavior in the thin-spined porcupine (*Chaetomys subspinosus*). Radio-tagged animals were never observed drinking water during more than 1,000 hours of observation.

The water-conserving strategy used by these two porcupine species is not known. One possibility is that the metabolic needs of the animals are satisfied by water contained in their normal diet of tree leaves. Katharine Milton reports that leaf-eating howler monkeys (*Alouatta palliata*) on Barro Colorado Island in Panama never travel to water sources, obtaining necessary water from their diets. A second mechanism of water conservation was explained by the classic work of the Schmidt-Nielsens. They showed that a number of desert rodents, such as kangaroo rats (*Dipodomys* spp.), manufacture their own water from the oxidation of carbohydrates in their dry seed diets. The metabolic oxidation of carbohydrates yields water and carbon dioxide as reaction products.

A third mechanism of water conservation has evolved in hibernating bears and other mammals. During hibernation, bears maintain near-normal body temperatures and metabolic rates, yet they neither drink nor produce urine while in this state. The major function of urine production in mammals is to rid the body of urea, the end product of mammalian protein metabolism. While harmless at normal blood concentrations, urea becomes neurotoxic at higher levels. How does a hibernating black or brown bear avoid poisoning itself? It recycles its blood urea with the help of intestinal bacteria, converting it into carbon dioxide and ammonia. The latter can be used to synthesize new proteins. By recycling its blood urea, the bear avoids the water loss associated with normal urea excretion.

Do porcupines recycle urea? Since porcupines do produce urine, it is unlikely that any possible urea recycling would approach the high levels (99.7%) recycled by hibernating bears. But even partial urea recycling can yield benefits in terms of water conservation and dietary nitrogen demand. Thus, Campbell and MacArthur of the University of Manitoba show that muskrats (*Ondatra zibethicus*) recycle 25% to 30% of their urea during fall and winter months, when dietary nitrogen levels are lowest. Muskrats are aquatic animals, and they are not recycling urea to cut down on water demand. Rather, they are cashing in on another benefit of urea recycling: reducing their dietary nitrogen demand.

Nitrogen (used to synthesize body proteins) is a key dietary nutrient for North American porcupines. They show their dependence on nitrogen in a multiplicity of ways: rapid weight gain in spring, when dietary nitrogen levels are high, and weight loss in the winter, when levels are lowest; feeding on leaf blades, where nitrogen levels are higher, and discarding the petioles, where they are lower; supplementing low-nitrogen foods such as fruits and mast with high-nitrogen foods in the form of tree leaves. Similar

nitrogen-seeking is shown by the thin-spined porcupine (*Chaetomys subspinosus*), which preferentially feeds on high-nitrogen new leaves and avoids lower-nitrogen older leaves. By recycling even a portion of their urea, such animals could significantly reduce their nitrogen demand.

At present, no porcupine has been studied with respect to urea-recycling ability. It would be interesting to see whether animals that must often cope with low-nitrogen diets and who may occupy dry habitats are using a technique that would reduce both stresses.

Chapter 8

Porcupines and Humans

Do porcupines make good pets?

Many people have kept porcupines as pets, and their experiences have varied. Ellis Potter from the Catskills region of New York recalls a baby porcupine kept as a pet. The animal had its breakfast with the family and occupied its own high chair, whose leg it would climb to reach the seat.

Another juvenile porcupine found a home with the Hassler family in the small Adirondack town of Childwold, New York. When young, the porcupine chased her tail like a puppy. She used to ride the family cat and played with it for long stretches. The dog would play with her as well but did not permit riding. The porcupine became the constant companion of the Hasslers' nine-year-old daughter Sonya, making many trips to school and to the neighbors. She never once bit or tail-slapped. The porcupine was allowed to go off in the woods by herself but always came back when called. She liked to ride on people's shoulders and suck the daughter's ear lobe, even when the porcupine got bigger.

When it came time to release the porcupine in the autumn and the family took her to the release site in the woods, she realized something was wrong when Sonya began to cry. The porcupine had been feeding on raspberry leaves, a favorite food. She dropped the raspberry canes, ran up to Sonya and started to cry as well, holding onto Sonya's leg. (Porcupine crying sounds remarkably like its human equivalent.) Roger Hassler pried her off his daughter's leg, but then the little porcupine wanted to cling to his leg instead. Eventually, the Hasslers left the porcupine in the woods. Whether such reintroductions of pet porcupines back into the wild are

successful is unknown, as I note in my 2009 book on porcupines; wildlife rehabilitators do not see released animals again.

Baby porcupines have a gentle, trusting temperament that lets them fit in easily with human families and other pets. But unlike puppies and kittens, porcupettes grow up to be wild animals. An adult porcupine becomes restless and potentially aggressive during the fall mating season. And despite their solitary lifestyles, porcupines respond strongly to each other, much as a human child raised by an alien species might respond to another human.

For these reasons, an adult porcupine kept as a pet might be well-fed and physically healthy, but it might prefer life in the wild. In the United States, a number of states have laws prohibiting the keeping of wildlife as pets.

In the words of Louise Erdrich: "An Ojibwe friend of mine named Delia, from Manitoulin Island, once had a porcupine for a pet. She told me that the little fellow liked to drink coffee and milk from a cup that it held in its paws. Nevertheless, I would not recommend taking a porcupine home for a pet. I would suggest an innocuous and harmless creature like a guinea pig, or at prickliest, a hedgehog."

Should people feed porcupines?

It is not easy to tempt a porcupine with food, especially in spring and summer when its natural diet is so rich that the animal is putting on weight at a spectacular rate. But in winter, when North American porcupines are starving and losing weight on a diet of tree bark, they will accept supplemental food, and I offer it whenever I can. One of their favorite foods is apples, preferably a sweet, low-acid variety such as Red Delicious.

Years ago, when I was following a population of radio-collared porcupines in the Catskill Mountains of New York, I reasoned that I should offset the cost to the porcupine of carrying a radio collar by offering an apple or two when I visited each animal at weekly intervals. Most animals were deep inside their winter dens, but my crunching steps in the snow did not go unobserved: the activity sensors of their radio collars cycled into the active mode. Yet the animals remained deep in their dens. I would drop the apples at the den entrance and retreat to watch. No porcupine would emerge, but at my visit a week later, the apples would be gone.

Porcupines are conservative about accepting new foods and taste them cautiously at first. But as the winter wore on, the animals began to anticipate my visits. When I dropped my apples at the entrance and withdrew to watch, a head would emerge from the dark entrance, and then a porcupine would pick up an apple and withdraw back into the shadows. Then soft chewing sounds could be heard.

At this time, one young male was spending daylight hours up a tall maple just downhill from his den. I left the apples at the base of the tree and would find them gone at my next visit. But after a few weeks, my approach would send the male into eager descent while I was still directly below. Would he have taken the apples from my hand? Because I did not want to accustom him to humans, I would withdraw before he reached the ground, where he consumed the apples as I watched.

As these examples illustrate, feeding North American porcupines is easy outside their winter dens. Extra calories in the winter can make the difference between survival and starvation. Death by starvation is typically observed in late winter, when calorie intake is down because of low food quality and calorie expenditure is up because of the need for maintaining body heat.

Some people inadvertently engage in a second kind of porcupine feeding, supplying them with sodium. Sodium-seeking is a major mortality factor for porcupines in the spring, as animals in sodium-depleted areas travel to highways and roadways to consume residual road salt. The porcupines involved are overwhelmingly females, whose sodium drive is heightened by both pregnancy and lactation. Unfortunately, porcupines and speeding cars can't coexist.

Sodium seeking in North American porcupines peaks in May. Porcupines' salt hunger cannot be satisfied by spreading salt on the ground. This creates a salt lick that attracts deer. Fish and game laws make the practice illegal in most states. Porcupines prefer another form of sodium presentation: scraps of plywood. Porcupines will gnaw these for their sodium content, while deer leave them alone. Once the first porcupine discovers the plywood, others soon follow.

Since the porcupines outside North America have a tropical to semitropical distribution, they do not suffer the winter period of food deprivation and weight loss experienced by the North American porcupine. For this reason, food offerings would not seem to have a critical importance. But like their North American cousins, all porcupines of the world are herbivores and therefore can suffer a sodium deficit. The plywood sodium offerings so gratefully accepted by North American porcupines might find equal acceptance everywhere else that porcupines roam.

What should I do if I find an injured porcupine?

Treating an injured porcupine is harder than treating an injured human. The human can explain his or her symptoms; a porcupine cannot. A human being can be fed a nutritious diet while convalescing; most people are not familiar with porcupine dietary requirements.

Fortunately, across the United States and Canada, and in other "porcupine" countries across the world, there is a network of people able and willing to help: the wildlife rehabilitators, a group of licensed practitioners with training in wildlife rehabilitation. In the United States, rehabilitators are licensed by their state fish and wildlife departments (or the environmental conservation equivalents). It is unwise, and frequently illegal, to attempt rehabilitation oneself, rather than turning the injured animal over to a licensed rehabilitator. Moreover, many states have laws prohibiting the acquisition of wild animals, whatever their condition.

An injured porcupine can be picked up in a container such as a plastic cooler or a kitchen-sized garbage can with a lid. Most injured porcupines will allow a human to approach and move them into a holding container with the aid of a broom or a shovel. (The Igloo cooler has its own closing lid.) It is then important to keep the animal in a warm, dark, quiet place till a rehabilitator can be contacted.

Most state departments of conservation or fish and wildlife will provide a list of rehabilitators and their specialties (songbirds, amphibians, small mammals, larger mammals, etc.). Rehabilitators often work with veterinarians, who can provide X-ray services, drugs, and anesthesia.

Rehabilitators are not allowed to charge a fee for their services; most subsidize their work from their own resources. Therefore, a contribution is a thoughtful gesture. To contact rehabilitators outside the United States, see appendix B.

What should I do if I find a diseased porcupine?

Few porcupine diseases display an unambiguous set of symptoms. And there is a danger of overdiagnosing disease where none exists. Porcupines with a wide range of parasites such as lice, gut nematodes, and tapeworms are not sick and don't require treatment. Porcupines that appear lethargic may simply be drowsing (the animals are normally active at night).

One porcupine disease that does present clear symptoms is scabies, which leads to death if untreated but for which simple and successful treatment is available. The animal's belly, face, and limbs become thickly crusted and brittle, so that movement and tree climbing become difficult or impossible. Even with scabies, however, the animal must be immobilized or anesthetized for treatment. For these reasons, and to comply with state legal requirements, it is important to leave treatment to a licensed wildlife rehabilitator. A rehabilitator will also be able to distinguish real disease symptoms from imaginary ones.

How can I see porcupines in the wild?

The North American porcupine ranges across most of Canada. In the United States, it is found in Alaska and in a broad western band from the Pacific east to the Dakotas and in western Texas. An eastern population is found in the New England states and parts of New York and Pennsylvania, but porcupines are absent from the Midwest to the Atlantic (Iowa to Delaware in the east) and from the Southeast (Louisiana to Florida in the east).

Porcupines are not evenly distributed within their species range. They are not found in areas of extensive farmland or around urban centers like Toronto or Buffalo. A good indicator of porcupine presence is the finding of roadkills in spring months. Porcupines seek residual road salt along highways and are cut down by passing cars. If no roadkills occur over an entire season, it is unlikely that porcupines will be found in surrounding woods.

To see live porcupines in the wild, you have to spend time in the wild, hiking in unbroken woods and looking up in the trees. In the summer, a porcupine high up in a tree is essentially invisible. Even if you know that a radio-collared porcupine is up a specific tree, you may have to spend a quarter hour carefully circling the tree and scanning it with binoculars before you spot the porcupine.

Porcupines are more easily seen in spring, before leaf-break, and in the fall, after leaves have fallen. Their dark bodies stand out in the canopy, though in a giant maple or beech a porcupine pressed against the trunk may look just like a knot in the wood.

Ordinary walks in the woods will bring random sightings, but the odds of seeing a porcupine under such conditions are low. Porcupines are solitary and have large nonwinter home ranges (a 50-acre minimum for females). To increase such odds, you should imagine the world of the animal you want to observe. The Chilean biologist Ricardo Martinez recounts a meeting as a student with the distinguished mammalogist Oliver Pearson at an ecology course that Pearson was teaching in Chile.

The students had been up much of the night, setting out 400 Sherman live traps for small mammals. In the morning they checked their traps and found just a single catch, a small bird—a success rate of a mere 0.25%. Martinez asked Pearson if he could accompany him, and the two walked about as Pearson set out some traps of his own. When they came to a bamboo, Pearson pulled out a small folding museum live trap from one pocket, baited it with oats pulled from another pocket, and walked on. On reaching a grassy area, Pearson stopped and searched with his hands, then parted the grass and showed the student a mouse "runway," in which he set another trap. At the end of the walk, Pearson had set just eight traps. But when he

Porcupine in a beech tree, early spring. At a time when rising temperatures bring porcupines out of their dens but summer foliage does not obstruct the view, the animals can be easily spotted in the woods.

and the student checked them later in the day, they found five mice of three species in the traps, for a success rate of 62.5%. Pearson had been "thinking like a mouse."

Similarly, you can enhance the odds of seeing a porcupine by "thinking like a porcupine." Porcupines are often hard to find in the winter because they are deep in their dens and out of sight. But on sunny days, porcupines may emerge and sun themselves in nearby trees. To come across those trees, you must locate the dens of the animals.

Porcupines prefer denning in hilly areas with exposed rock faces. The dens are located in natural crevices that reach deep into the ground. (North American porcupines do not excavate their own dens.) Active dens will be signaled by debarked trees and saplings in the den vicinity. How can you determine whether the den is active? Check the entrance for fresh porcupine tracks in the snow. Porcupine tracks are unmistakable, easily distinguished from the tracks of other animals by their large footpads and very short footsteps.

In late winter and early spring, when temperatures are rising but snow remains on the ground and tree buds have not begun to swell, porcupines are often found in hemlock groves, which offer them both food and shelter. To find a porcupine in a hemlock grove, look for porcupine snow tracks and follow the tracks to their terminus at a hemlock tree. Further signs of occupancy will come from porcupine droppings under the tree and branch fragments cut by the porcupine.

In the summer, porcupines are hard to see in high treetops. But it helps to know they often feed in aspens and lindens, rare species in a forest.

North American porcupine feeding trail in the snow. The animal traveled from its den to the base of a small hemlock tree (left-hand trail), climbed the tree to feed in the canopy, then returned via the right-hand trail. Drops of urine lie in the return trail. The winter feeding behavior of the porcupine can be precisely mapped by following its trails in the snow.

Check the ground below these trees for feeding signs in the form of nip twigs—twig tips cut from a main branch, with leaf blades removed but petioles intact. If the nip twigs are fresh (not brown or wilted), look in the tree carefully; the porcupine may still be present. Fresh nip twigs in the summer are one of the few "hot" clues to porcupine presence. By thinking like a porcupine, you will encounter them where they live and raise their young.

What if you want to encounter a South American or Old World species? The bar will be raised many notches. Voss and da Silva have described the difficulties of capturing small South American porcupines in the wild. They note that as a last-ditch effort, collectors have captured porcupines by pulling them out of their odoriferous dens.

Gaston Gine, of the State University of Santa Cruz in Brazil, who studied the thin-spined porcupine, *Chaetomys subspinosus*, locates new porcupines by scanning the canopy. Each porcupine captured requires, on average, 22 hours of searching; radio-collared animals who have been tracked to a specific tree can be seen from the ground less than half the time. In the future, he hopes to locate porcupines by training a dog to detect porcupine feces.

One indirect method that has been used by South American hunters is to wait at night near a natural salt lick. Many herbivores come to ingest salt at night. Louise Emmons reports that the list includes South American porcupines.

Such indirect methods may also work with Old World porcupines. In Malaysia, Miura and coworkers set up an infrared-triggered camera to record visitors to a fallen-fruit cache under a tree (the cache was artificially

replenished by the scientists). The camera caught frequent visits by the long-tailed porcupine, *Trichys fasciculata*, and less frequent visits by the Himalayan porcupine, *Hystrix brachyura*. The camera also recorded the times of the visits. All visits were at night and peaked at midnight. Old World porcupines are more strictly nocturnal than New World forms and therefore less easy to observe in the wild.

Why are so many porcupines found as roadkills?

As noted above, North American porcupines and speeding cars don't coexist. The reason is rooted in evolutionary theory.

The biologist Garrett Hardin has pointed out that skunks are maximally successful when behaving boldly, cottontails when timid. Bold temperaments allow skunks to take advantage of a range of feeding opportunities, and their powerful odor defense lets them get away with behaviors that would doom a cottontail. It is therefore not surprising that both skunks and porcupines are overrepresented among roadkills. Both use a defense system effective against a fox when confronting a car.

Porcupine responses to cars would be comical if they weren't so often tragic. In one car-porcupine encounter, I was driving at night along a country highway. Ahead of me, a porcupine appeared in the headlights, walking slowly along the middle yellow line. I slowed to a crawl, pulled up behind the porcupine, and blew my horn. Instead of scurrying into the brush, the animal whirled, erected its quills, and stood its ground. Evolution and technology move at different speeds.

Chapter 9

Porcupine Problems (from a human's viewpoint)

Are some porcupines pests?

Conflicts between humans and porcupines are real and continuing. In North America, human-porcupine conflicts take two forms: conflicts due to porcupine salt-seeking and conflicts due to porcupine winter feeding.

Porcupines seek salt (sodium) for fundamental physiological reasons: their all-plant diet does not contain the sodium needed for muscle and nerve function and for nursing their young. This is a problem faced by all herbivores, including deer, moose, buffalo, bighorn sheep, woodchucks, and many more. All herbivores must seek supplemental sodium supplies to stay alive.

North American porcupines seek their salt from human-associated sources, which they do not recognize as dangerous. Porcupines have invaded our cabin in the Catskill woods some four times over the past decade. Each time, the animal tore a hole in the screen of a basement window. The havoc a single porcupine can cause inside a house or cabin is astonishing: water cans and paint cans overturned, a pitchfork and shovel torn off their hooks on the wall, a mess of overturned jars on the workbench, the contents of a wall cabinet dashed to the ground, porcupine droppings on top of the refrigerator, a windowsill gnawed as the animal struggled to get out again. It did so by pushing out a window screen from the inside. While the resulting mess was considerable, I worried more about the porcupine. What would have happened if the animal had invaded a house that was occupied, and not by a porcupinologist?

More commonly, when porcupines visit houses and sheds near the edge of the woods, they remain outside, where they use their powerful incisors to

gnaw plywood and the neoprene tires and hoses of cars and farm machinery. The sodium of plywood is in the resin, a polymer manufactured with a sodium hydroxide catalyst. The industrial synthesis of neoprene (artificial rubber) likewise involves sodium as a minor component. A night's chewing can disable a car's tires and electrical system. Damage to plywood is slower to accumulate, but a week's repeated chewings will be easily visible. The damage is seasonal. The porcupine's salt drive peaks in April through June and becomes nonexistent in late fall and winter.

Salt-seeking behavior extends to the South American porcupines as well. Louise Emmons reports that *Coendou* species commonly visit mineral licks. And one juvenile Brazilian porcupine entered her jungle camp to lick the frying pan, presumably for its salt. (See color gallery 2, page 5.)

Porcupine damage to trees in North America follows the opposite time course, peaking in winter, when the animals feed on tree bark. If a tree is girdled at the base, it will die because phloem can no longer bring nutrients to the roots. As my 2009 study of New York porcupines reports, 95% of the bark damage occurs higher in the tree, where individual branches may die while the tree becomes misshapen but continues to live.

Statistics such as these will be of little comfort to people whose trees are damaged or killed, especially when the trees have been planted or grow close to the house and form a beloved landscape. Trees in a porcupine's environment are subject to costs similar to those associated with a street tree in the city. The street tree may shed branches, may cover the lawn with leaves, or may get uprooted by storms and ice. We accept such costs because a city without trees is less rich and satisfying to live in. There are steps short of killing the porcupine that can save their trees (see "How can I keep porcupines away from valuable trees?").

Not everyone will agree. An article by Khan and coworkers in the ominously titled journal *International Biodeterioration and Biodegradation* discusses the Indian crested porcupine (*Hystrix indica)* in Pakistan. It states that the porcupine "has been identified as a serious pest of traditional as well as non-traditional crops, fruit orchards, vegetables, flowering plants and grasses of foraging importance in rangelands." The porcupine is also accused of damaging forestry and reforestation areas. Research is needed on porcupine repellents where conflicts occur.

Why do porcupines sometimes gnaw the rubber tires of cars?

Most cars roll on tires of synthetic rubber. The industrial development of synthetic rubber required contributions from chemists across the world, and some call the synthesis the crowning achievement of twentieth-century

"Witch trees" in the vicinity of a North American porcupine den. The porcupine's long-term winter feeding in the canopies of surrounding trees has given them a brushlike appearance.

organic chemistry. The synthetic pathway is very complex; and tire rubber, besides its styrene and isoprene carbon skeletons, requires the use of a number of sodium salts, which remain locked up in the final product. It is these sodium traces that the porcupine can detect and that it tries to absorb by chewing on tires and rubber hoses.

Porcupines do not generally approach cars that have been recently used; perhaps the smell of fresh exhaust products is a deterrent. But when cars or tractors remain in place for longer, their tires may start to show the grooving of powerful porcupine incisors.

Some residents of the Catskill Mountains of New York with porcupines in close proximity build cyclone-fence cages for their cars. And one Catskills farmer, trying to keep porcupines far from his machinery, has deposited an old tractor tire deep in the woods, where it has lain for decades but continues to receive fresh porcupine tooth marks every spring.

How can I keep porcupines from my cabin in the woods?

Porcupines don't chew cabins to eat wood, which they can find in abundance in the forest, nor to sharpen their incisors. They come to cabins to seek sodium, and they find it in the resins of plywood and in plywood-based house sidings. Sodium will also be present in outhouses and in other salt- or urine-stained structures.

To keep porcupines away from plywood siding, the cheapest, least labor-intensive method is to staple a 3-foot strip of 1-inch chicken wire all

Porcupine cage for a car. This wire cage in the Catskills keeps the car in, the tire-chewing porcupines out.
Photo by Laura Anthony.

around the base of the cabin. Three feet is about as high as a porcupine on the ground can reach. Though porcupines can climb the chicken wire, they don't generally try to. You don't have to allow for the height of the snow pack because cabins are attacked in the spring, after snow has melted.

Thick exterior paint over the plywood will also sometimes stop porcupines. If they can't taste the sodium on the surface, they will not chew further. But once a small area is scraped off and the underlying plywood exposed, porcupines will enlarge the breach. A more permanent solution involves the application of wood or vinyl siding over the plywood. Neither material contains significant sodium, and porcupines will not chew through the siding to get to the plywood below. That is to say, porcupines can't detect salt at a distance.

Still another strategy is to deflect the porcupines by leaving plywood scraps on the ground a little distance from the house. The plywood should be placed in the direction from which porcupines might be expected to come at night—the woods. Check the scraps regularly, for once the porcupines have discovered them, the material is consumed surprisingly quickly.

Remember that porcupines are rodents, who obtain their sodium supply by gnawing. Salt left directly on the ground will not attract North American porcupines but will draw deer and other salt-seeking herbivores.

Can there be too many porcupines in a forest?

The honest answer seems to be no. There are two reasons that porcupines don't seriously damage forests.

First, female North American porcupines maintain exclusive territories from which other females are excluded. Even at peak population densities,

Male North American porcupine at salt source. The plywood walls of this cabin are protected with a roll of chicken wire. Porcupines come to chew on salt-impregnated wood sticks (light color) and leave the rest of the cabin alone. Porcupine salt-seeking from human sources is one of the chief causes of human-porcupine friction.

the territories remain large enough to support the porcupine and her offspring. When a newly dispersed female tries to establish a territory of her own, she must keep searching until she finds an unoccupied corner of the forest. She cannot double up with a resident female, even her own mother. Established females stay on their territories for life, even into extreme old age.

Second, porcupines have a low reproductive potential. Instead of the hundreds of eggs laid by a destructive forest insect, a female North American porcupine produces just one offspring a year. This means that the porcupine population grows slowly, if at all, and cannot easily overshoot a limit that would damage the forest.

How can I keep porcupines away from valuable trees?

The most effective porcupine defense is to encircle the tree trunk with aluminum flashing stapled to a height of 3 feet above the ground. Remember that ground level may rise in the winter by the height of the snow pack, so flashing should reach 2 feet above the usual snow pack height. The aluminum prevents porcupines from climbing the tree by denying them a claw-hold. Aluminum flashing comes in various widths and is available in hardware stores and masonry and roofing supply stores. To make the material less unsightly, you can paint it a dark color, but the paint layer should

not be thick enough to provide a claw-hold for the porcupine. Flashing should be applied before the winter, since porcupine bark-feeding begins after leaf-fall.

There is no need to apply flashing to trees that porcupines don't use in the winter. Most prominent of these is red maple, whose high tannin content deters porcupines. Other trees seldom used in the winter include white ash, hickory species, and ironwood. By contrast, sugar maple and striped maple are winter favorites. Beech, oaks, and linden are also vulnerable, as might be any number of exotics. Hemlock is used as a winter food but not via bark chewing; porcupines cut small terminal branches and consume the needles.

Protecting large numbers of trees by the use of flashing is economically prohibitive. An alternative is to install a fence around the trees at risk with a hot wire 2 inches above the top. Or you might consider an approach, described by Ziegltrum, that is used by lumber companies to limit black bear damage to tree plantations.

When black bears emerge from hibernation in the spring and can't find other food, they will girdle trees at the base and consume the nutritious inner (phloem) layer. Because bears are larger than porcupines and feed in a less efficient manner, they can do far more damage: a single bear can damage or destroy 70 trees a day. To mitigate the problem, the USDA Animal Damage Control Program, which is supported by the lumber industry, has worked in Oregon and Washington State to establish bear feeding programs during the critical months. Similar programs are in use in China, Japan, and Croatia. The programs have been highly successful in limiting tree damage but have increased local bear populations. The feeding program uses automatic feeders dispensing a pelleted chow created for bears.

Several kinds of rodent chow are commercially available that could be used in feeding stations for porcupines. Automatic wildlife feeders available from hunting stores and forestry supply houses dispense corn or various pelleted foods on a daily schedule. If you use this method, you may also be feeding local hares, deer, wild turkeys, and other animals, whose population densities can be expected to rise. Paradoxically, the method will probably not increase local porcupine densities, since porcupine females are territorial.

Are porcupines dangerous to people or pets?

Despite their gentle and trusting nature, porcupines can be dangerous to people, and more so to pets. This follows not from any innate aggressiveness of the porcupine, but from the misunderstandings of first encounters between people, their pets, and wildlife. The wild animals that share the woods with porcupines are for the most part well aware of the por-

Defensive position in a spruce tree. This North American porcupine presents its back to the enemy. The erected quills of the back and tail-driven quills below make the porcupine in a tree invulnerable to most predators.

cupine's defense capabilities and leave it alone. In the Catskill Mountains of New York, I have seen dozens of wild raccoons, yet only one animal showed evidence of a porcupine encounter—a half-dozen quills stuck in its muzzle and nose.

The situation is different when pets, especially dogs, have a first-time porcupine encounter. The dog who has had no experience with porcupines may attack it or try to move too close, with devastating consequences. The most grievous punishment is inflicted on dog breeds such as pit bulls, who do not take a hint but persist in their attack. Before the battle ends, the dog may have hundreds to thousands of quills piercing its muzzle and face. The most dangerous quills are those that have reached the eyes; these can lead to a detached retina and loss of sight.

A retrospective veterinary study by Johnson and coworkers in 2006 found that the dog breeds that were overrepresented in terms of quill injuries were the "aggressive" breeds: Siberian huskies, rottweilers, and German shepherd mixes. The areas most often quilled were the head and the neck (265 of 296 cases) as well as the mouth (211 cases). Most quills were successfully removed, but a special concern was the internal migration of quills or quill tips. In 6 of 296 cases, the quills migrated to leg joints, leading to lameness. In 4 cases, they migrated to an eye. In half of those cases, the eye had to be removed.

Cats are less likely to suffer quill injuries simply because they are less likely to take walks in the forest, but they are predators and might con-

The result of a dog-porcupine encounter. Despite the large number of quills in its jaw and face, this pit bull has been relatively lucky. Most of the quills have been lightly embedded, and none have struck the eye or the inside of the mouth. Photo by Samantha K. Yeltatzie, DVM.

sider a porcupine a target. I got a demonstration of this in 2003, when I was raising a baby porcupine whose mother had been road-killed. The baby was walking slowly in our back yard when I noticed a neighbor's cat creeping through tall grass, in the final stages of a stealth attack. I saved the porcupine and therefore saved the cat. Quill injuries in cats often involve the paws, since cats try to swat their prey. On the other hand, the story of a pet porcupine's relationship with Roger Hassler's cat (page 123) shows that porcupines, especially baby porcupines, can coexist harmoniously with family pets. Unfortunately, porcupines in the wild don't have an opportunity to build relationships with pets.

What porcupines in the wild can do to pets, they can do to humans. In a worst-case scenario, the quill can disappear beneath the skin and travel through the body; in such instances, one must hope that it emerges before hitting a vital organ. As I can testify, the pain is intense during the entry and travel periods, but painless on exit.

Most quilling encounters involve wild porcupines defending themselves, but accidental quillings can occur even with tame porcupines. Ann Bryant, a wildlife rehabilitator in California, was accidentally quilled while playing with an injured male porcupine she had rehabilitated following a car accident. The injuries had permanently crippled the porcupine and prevented its release back into the wild. Over the years the two got very attached to each other, going on walks together, sometimes with the porcupine riding in a wagon.

One day Ann was playing with the male, flipping him on his back and

Porcupine quill tip emerging from a knuckle. The quill entered on the palm side, breaking off on entry. The tip traveled through the knuckle, propelled by one-way barbs. A thin coating of quill antibiotics prevented an infection.

tickling his belly, a game he loved. Ann says she got careless and a quill entered the back of her hand. In her words,

> it went under the skin right away and formed a huge bulge that was extremely painful. The pain was so great that I let a friend bring me to the ER. The doctor cut my hand open and dug all over … but couldn't find it. By the time the numbing agent wore off the pain was mostly gone. I could feel it in there but it wasn't bothering me. Then, a few days later I started to feel it move up my arm. It went all the way up to my shoulder and I got worried that it was heading for my brain or my heart and another friend who is a retired doctor insisted on taking me in for tests to find it. We made appointments and within the time it took for the first appointment the quill went back down to my wrist (I could feel it moving). We went in to several labs and had X-rays, Ultra Scans, magnetic resonance scanning and even a mammogram of my hand and wrist! But nothing could be seen in any of the tests so there was nothing more we could do. I continued to feel it in my wrist (it never moved again) for about three years. Now, the only lingering sign of it ever having happened is that I can't bend my wrist as far as I could before and it's slightly weaker than the other one. I imagine my body absorbed it which is just fine with me because I can now proudly say I am part porcupine.

Ann Bryant's story had a happy resolution: the quill turned around at her shoulder, perhaps because it had been bent on initial entry. Others have not been so lucky. Quills are powerful weapons, and like all weapons can discharge when least expected. Children and pets in particular are at risk when interacting with adult porcupines.

Do porcupines transmit human diseases?

Porcupines are not known to transmit any serious animal-borne diseases such as rabies, Hantavirus, or Lyme disease, either directly or indirectly. In the western United States, porcupines are indirectly associated with one animal-borne viral disease, Colorado tick fever.

Rabies is a disease carried by infected raccoons, bats, foxes, skunks, and, rarely, household pets. The disease is transmitted by animal bite. Porcupines neither bite other animals nor get bitten. No porcupine has ever been recorded as being rabid. Porcupines do not serve as reservoirs of the deadly Hantavirus, which is spread by droppings, urine, and saliva of deer mice, white-footed mice, and cotton and rice rats.

Porcupines also are not vectors for Lyme disease, whose causative agent is the spirochete bacterium *Borrelia burgdorferi*. *Borrelia* is transmitted by the bites of infected ticks. The ticks in turn acquire the spirochetes from animal hosts such as deer and deer mice. The primary ticks associated with porcupines are *Ixodes cookei* in the east, *Dermacentor andersoni* in the west, and *D. variabilis* in the north. None of these serve as hosts for *Borrelia*.

The one animal-borne human disease for which porcupines can serve as hosts is Colorado tick fever (CTF). CTF is spread by bites of the tick *Dermacentor andersoni.* Besides porcupines, other hosts of this tick are rabbits and hares, ground squirrels, small rodents, foxes, coyotes, and mule deer. The disease is found mostly in the western United States, typically in mountainous areas such as Colorado and Idaho. Symptoms—including fever, headache, and possible vomiting—begin 3 to 6 days after the tick bite and last about 3 days. After a period of remission, the symptoms return again in heightened form for an additional 1 to 3 days. The disease resolves spontaneously and typically leaves no lasting aftereffects. Patients with CTF are typically campers or young males who have spent time in the woods.

In the early 1990s McLean and coworkers trapped 20 adult porcupines and looked at tick loads and anti-CTF antibodies in the blood. The porcupines carried large tick loads—an average of 25 adult ticks per porcupine. No virus was isolated from any of the porcupines, but 17 of them (85%) had neutralizing antibodies against CTF virus. The biologists surmised that porcupines are infected as juveniles, then develop antibodies, and become virus-free as adults.

Is it safe to eat porcupines?

Not necessarily. H. C. McDade and W. B. Crandall, in an article in the *New England Journal of Medicine*, describe a 1934 case of a man who ate

a porcupine-meat sandwich. Four days later, intense abdominal pain sent him to the New London, New Hampshire, hospital. Surgery revealed a quill-perforated stomach, with further internal stab wounds that had released intestinal bacteria into the peritoneal cavity. In 1934, no penicillin was available, and 8 days after the operation the man died.

The article describes a second patient 24 years later who had likewise ingested quill fragments. After experiencing severe intestinal pain, he was admitted to the hospital in White River Junction, Vermont, where surgery revealed a quill-perforated small intestine. After intensive penicillin and streptomycin therapy, the patient recovered.

In years before the European settlement of North America, the porcupine was a highly regarded food item among Native Americans. Some dealt with the quill problem in an ingenious way. After killing the porcupine, they singed it, then encased it in a clay cocoon and baked the product in a fire. The clay shell retained the quills and kept the porcupine meat moist and evenly cooked.

For tribes of the northeastern United States and the Canadian Maritimes, the porcupine held a special significance. It was one of the few animals the hunters could depend on in early winter, when ice foreclosed fishing but the deep snow required for the driving of moose and caribou had not yet accumulated. Because the hunters believed the porcupine offered itself to them, its bones were not fed to the dogs but burned or sunk in the river. The porcupine was so important to the Micmacs of New Brunswick and Nova Scotia and the Montagnais of eastern Quebec that these tribes were collectively known as the Porcupine Indians.

Erin Hasinoff from the University of Columbia Anthropology Department spent a month with the Innu people of Labrador, who have continued the ancient traditions and hunt porcupine and partridge in the winter. Hasinoff observed that "porcupine tastes like trees, and so does partridge. The meat actually tastes like spruce. If a vegetarian had to choose meat to eat, these would be the ones."

There is less meat on the North American porcupine than the size of the animal suggests. Muscle mass accounts for only 26% of body weight, as opposed to around 40% in typical mammals. Quills, skin, and the digestive tract make up more than 50% of the porcupine's weight.

Freeman, and Xavier and coworkers, show that all species of porcupine carry intestinal tapeworms. The meat should therefore be well cleaned and well cooked. Most importantly, the intestinal tract with its tapeworms should be removed intact.

The porcupines of Africa and Asia (brush-tailed porcupines, genus *Atherurus*, and crested porcupines, genus *Hystrix)* are highly prized as food, and their meat is commonly sold in local markets. Jori and coworkers sur-

veyed the hunting and consumption of the African brush-tailed porcupine, *Atherurus africanus*. They note that the animal is a favorite source of meat for urban and rural populations of Gabon, Nigeria, Cameroon, and the Congo. In Gabon, the porcupine accounts for 27% of the meat available in markets, despite generally commanding a higher price than other game or domestic animals.

In Africa the porcupine is hunted with cable snares set in the forest. The brush-tailed porcupine, along with three species of duiker (antelopes), make up 75% of the catch. One-third of the animals captured break their cables and escape with injury; about one-quarter of the catch is lost to scavengers or decomposition. Jori and associates feel the hunting intensity is too high to be sustainable and suggest a captive breeding program as an alternative.

How can I remove quills from a pet?

If you have ever removed a deep quill from your own hand or leg, you know how painful the experience can be. For dogs, the quills usually must be pulled from the head or mouth, an incomparably more traumatic experience. It is hard to imagine an animal holding still for the process; in fact, the head must be tightly immobilized by tying it to a post or other support. The quills should be removed with pliers or heavy-duty tweezers or a hemostat, held as close to the skin as possible.

Dogs may try to remove the quills by rolling on the ground or rubbing with their paws. This should be discouraged because the process will break and splinter the quills, making removal more difficult.

The hardest quills to remove are those in the mouth or tongue. The mouth gets quilled in two-thirds of dog-porcupine encounters. It is almost impossible to examine the area and remove the quills without chemically immobilizing or anesthetizing the dog. Once this is done, the dog's mouth can be kept open by locking its upper and lower canines into a dental gag. The anesthesia and mouth propping are procedures that only a veterinarian can carry out. Therefore, a dog with quills in its mouth must be seen immediately by a veterinarian. If all quills and quill fragments from the head or mouth areas are not promptly removed, they can migrate to vital organs, including the eyes.

For some dogs, a porcupine encounter is a lesson well-learned and never repeated. But owners report that a surprisingly large fraction of dogs don't learn: they repeat their porcupine attacks at the next opportunity. With such dogs, it falls on the owner to keep the dog on a leash when walking through porcupine country. If the problem is a porcupine that comes to the owner's house at night, the dog should be safely locked inside.

What should I do if I am injured by a porcupine?

North American porcupines defend themselves, not by biting, but by quilling their persecutors. Therefore, treatment of a porcupine-inflicted injury is almost always a problem in quill removal. Quills should be removed as quickly as possible. The longer they are left in place, the greater the possibility that a quill will ratchet its way deeper into the body, making removal more difficult and sometimes impossible.

A quill tip that is not properly removed can work its way beneath the skin and travel internally. Quill tips that enter through the fingers will generally travel through the flesh and exit on the opposite side. After a painful entry, the exit process is painless and is generally not accompanied by swelling or inflammation. Once the exiting quill tip has broken through the skin, it can be pulled out easily with tweezers. (Quills move easily in the forward direction, painfully backwards.) However, a quill in a knuckle may require a doctor's attention.

If quills are large and lightly embedded, they can be pulled out by hand. Quills that are more deeply embedded, or quills that are broken, should be pulled out with pliers or with heavy-duty tweezers, applied as close to the skin as possible.

One well-known mammal field guide declares that porcupine quills are hollow, and that embedded quills should be cut to let out the air and reduce quill diameter. This is dangerous advice. Quills are not hollow but are filled with a spongy matrix (medulla) that stiffens the quill. Cutting a quill will not reduce its diameter, but can splinter the quill shaft and make it more difficult to grasp with tweezers or pliers.

Quills can travel long paths in the body. I once had a quill disappear under the skin of my upper arm. The quill traveled down my arm, around the elbow, and emerged from the lower arm three days later. Had it moved in the opposite direction, emergency surgery might have been required. Treatment is complicated by the invisibility of quills in standard X-rays.

Can porcupines act as invasive species?

Examples of invasive species abound in the world. The nutria, established in the United States and southern Canada, was introduced from South America. The North American starling and the gypsy moth, now widely established on the continent, arrived from Europe. The same is true of some 20% of the North American flora. Apple trees, yarrow, moth mullein, yellow water lily, English and common plantain, dandelion, white and red clover, ox-eye daisy and chicory—all are of Old World origin. Native Americans, who were well aware of the floral influx, referred to the English

plantain as "white man's footsteps." The dispersal can go in the other direction as well: gray squirrel and muskrat are two North American immigrants now flourishing in Europe.

Can porcupines participate in similar faunal transfers? Indeed they can: Gosling describes an example of an Old World porcupine establishing itself far outside its normal species range. The species involved was the Himalayan porcupine, *Hystrix brachyura*. In 1969, two animals kept in a menagerie in Devon, England, escaped and established a breeding population in the wooded valleys of the rivers Oakment and Torridge. There, the animals ran afoul of local forestry interests. To supplement their normal diets of bulbs and tubers, they damaged tree bark in a conifer plantation. The population was exterminated.

Was *Hystrix brachyura* in Devon a threatening invasive species? Its origins were exotic, and it was causing damage in a timber plantation, itself an unnatural landscape. Devon is a densely settled, thoroughly developed countryside. Had the porcupines escaped to the wild highlands of Scotland, would their fates have been different?

Human Problems (from a porcupine's viewpoint)

Are any porcupine species endangered?

The International Union for Conservation of Nature (IUCN) lists *Chaetomys subspinosus*, the thin-spined porcupine, as "vulnerable"—one step short of "endangered." The population numbers of this species are decreasing. *Chaetomys* had not been sighted since 1952 and was thought to be extinct in the wild, when in 1986 it was rediscovered by Ilmar Santos, a Brazilian biologist. The porcupine's habitat, the Atlantic coastal forest of Brazil, has been 92% destroyed by lumbering, agricultural clearing and urban sprawl. The destruction is continuing.

The Atlantic coastal forest stretches along the mountainous eastern coast of Brazil from Recife in the north to the borders with Argentina and Paraguay in the south. The forest is separated from the Amazonian rain forest to the west and north by savanna and desert scrub. The coastal forest is one of the biologically richest areas of the world, and has been designated a World Biodiversity Hotspot. Wait Thomas, a botanist at the New York Botanical Garden who has devoted his career to the study of the rich flora of the coastal forest, tallied the tree species greater than 2 inches (5 cm) diameter at breast height on 2.5 acres (1 ha) of the forest. He and his team identified over 450 species. By comparison, the entire eastern United States, from Maine to Florida, has only 232 tree species.

The naturalist Alex Shoumatoff describes a visit to the Atlantic Forest in the province of Bahia:

> Caititú happened to be the very forest where Wait Thomas and his team identified more than 450 species of tree. Most of the trees were only 30 or

> 40 feet tall and not very thick, because the soil was thin and lateritic, but there were a few gigantic, buttressed maçarandúba and citão trees. Their straight boles were strung with a seething chaos of vines and encrusted with epiphytes. I had never seen such a diversity of leaf shapes and plant types in any rainforest, so many forms of life, many of them reduced, that were new to me, so many microhabitats and microniches, miniature vines with intricately filigreed leaves, and frogs no bigger than your fingernail. A strikingly striped slug-like Geoplanario in a pool of water in a bristling ground bromeliad. The Mata Atlântica, Antônio said, is the world center of bromeliad diversity. There are over a thousand species. This is where the pineapple family originated. We crept toward something big thrashing in the understory, hoping it would be a monkey, but it was a just-fledged filhote de urubú, a juvenile black vulture, getting its wings tangled in vines.

More than 20,000 vascular plant species are found in the Atlantic Forest (with more being discovered), including trees, vines, bromeliads, ferns, grasses, and forbs. Because of their geographical isolation, 40% of these are found nowhere else on earth. In addition, 576 of the forest's 1,361 vertebrate species (birds, mammals, reptiles, amphibians) are endemic to the area.

But of the forest's original area of 474,780 mi^2 (1,230,000 km^2) of the forest, only some 8% is left. The reason is that the moist, fertile coastal zone is also prime human habitat: 70% of Brazil's population is located here, including two of the country's largest cities, Rio de Janeiro and São Paulo. The threats to the forest are widespread: logging, agricultural clearing, urban spread, road building, hunting, the palmito industry (which kills palm trees to extract the edible hearts of palm). Of the 202 animal species threatened with extinction in Brazil, 171 are in the Atlantic Forest.

It is in this forest that the thin-spined porcupine makes its only home. It shares the forest with the Bahia dwarf porcupine (*Coendou insidiosus*). In the southern part of its range, it also comes in contact with Paraguayan porcupine, *C. spinosus*. The latter two species appear to be maintaining stable populations. What sets *Chaetomys* apart? The sad fact is that our understanding of the natural history and habitat requirements of South American porcupines is shockingly low. In the words of Louise Emmons, "There has been no in-depth study of any [South American porcupine] species, and for most there is no published natural history at all."

At the time of this writing, a number of radiotelemetry studies of *Chaetomys* have been initiated. Both the study by de Souto Lima and coworkers, and that of Gine and coworkers, find that individual animals have specialized diets. However, the preferred feeding trees are fairly abundant in the Atlantic Forest, so food supply does not appear to be the limiting factor in

Chaetomys's decline. An ecological understanding of the situation will require further studies.

The IUCN verdict on three other New World porcupine species neither sounds an alarm nor issues a clean bill of health. These species—*Coendou vestitus*, the brown dwarf porcupine; *C. roosmalenorum*, Roosmalen's porcupine; and *C. ichillus*, the streaked dwarf porcupine—are given question marks; our information on them is "data deficient." We don't know whether the populations are holding steady; we don't have a good idea of species ranges; we have little information on feeding habits, social structure, evolutionary relationships, ecological tolerances. But we do know that everywhere, their forests are under threat.

In contrast with the poor database for South American porcupines, a rich museum record exists for the North American porcupine, and I used the museum record to gauge human impacts on the North American porcupine population. I reasoned that animal species under strong hunting pressure (such as the great whales prior to the International Whaling Commission's whaling ban) would show a skewed age distribution. As long-lived individuals are lost, the life expectancy goes down. I compared two porcupine populations: 33 animals from pre-1903 Alaska, Yukon, and Idaho (areas with low human density); and 20 animals from post-1950 New York and New England (higher human density). I estimated porcupine life expectancies by looking at the frequencies of very old individuals as gauged by tooth wear. The pre-1903 population contained 4 very old individuals; the post-1950 population contained 3. The old-age frequencies are statistically indistinguishable. It therefore appears that humans have had little influence on North American porcupine life expectancies.

How does this picture compare with ecological stresses faced by the Old World porcupines? For one species, the Philippine porcupine (*Hystrix pumila*), the IUCN has raised its rating of risk from "least concern" to "vulnerable." The major reason is much the same as for the thin-spined porcupine: loss of forest habitat. In addition, Philippine porcupines are hunted for bush meat and collected as pets. But in contrast to the thin-spined porcupine, Philippine porcupines can also forage in grasslands, scrublands, and cultivated areas.

For other Old World porcupine species, the outlook seems less threatening. Some species, such as the Indian crested porcupine, *Hystrix indica*, are so successful that active removal campaigns are waged by farmers.

The survival of the *Hystrix* porcupines is noteworthy because they can sometimes coexist with dense human populations. The population of Himalayan porcupines (*H. brachyura*) in Hong Kong provides an example of such coexistence. Hong Kong is a South China territory of 425 mi^2 (1100 km^2). With a human population of 7 million, it is one of the most densely

settled areas of the world. The landscape is subtropical and intensely degraded, the result of at least 7,000 years of continuous human settlement.

To survey the surviving populations of larger mammals in Hong Kong, Pei and coworkers set up a network of 373 camera traps that logged 1.4 million camera hours of observation and recorded 20 mammalian species in 9,215 photographs. The wild animals most often photographed were Himalayan porcupines, which generated 1.3 pictures per 1,000 camera hours of observation. The porcupines are probably survivors of Hong Kong's primeval fauna. Why did these animals survive when other groups such as flying squirrels, many primates, tigers, bears, and elephants did not? The Himalayan porcupines are not dependent on forests but can survive in open habitats.

The Hong Kong example carries a mixed message of survival and loss. Its tropical forest survives only in small fragments, and many forest-dependent animals have disappeared, but the territory remains home to 27 species of terrestrial mammals (some too small to show up in the camera traps) and 26 species of bats. Although Hong Kong is densely settled, the human population is concentrated in urban enclaves. Over 40% of the land is protected, maintained as forest fragments or open grasslands. The local porcupines face no hunting pressure, something not true in other parts of their species range.

Will porcupines be affected by global warming?

Global warming, in a historical sense, has provided the warmth needed to maintain life on earth. But when warming reaches the levels predicted for 2100, the biological systems of the world may suffer multiple and unexpected changes. Porcupines are part of these systems.

Global warming is generated by the greenhouse effect, first explained by the nineteenth-century Swedish chemist Svante Arrhenius. The atmosphere contains gases such as water vapor, carbon dioxide, methane, and ozone that are transparent to visible light but opaque to infrared radiation. These are the greenhouse gases. When the earth absorbs a photon of light from the sun, the photon is typically re-emitted not as light (because the earth is not a mirror), but as infrared radiation, which we sense as heat. Because the greenhouse gases block the passage of infrared radiation, the earth today is warmed, on average, by about 59°F (33°C), the margin that makes life possible.

Since the beginning of the Industrial Revolution, human activities have steadily raised the atmospheric concentration of one of the greenhouse gases, carbon dioxide. This increased CO_2 concentration is, in turn, raising the average temperature of the earth. Because global warming creates

powerful feedbacks, the scenarios for the future are not linear extensions of the past but must be modeled with sophisticated computer models. Essentially all the major feedbacks are positive: global warming accelerates further warming.

Global warming will affect both arctic and tropical environments. In the Arctic, melting of circumpolar permafrost (frozen ground) will make large amounts of organic carbon available to bacterial degradation and release in the atmosphere. E. A. G. Schuur and coworkers estimate that Arctic permafrost holds 1672 petagrams (Pg) of carbon (1 Pg = 1 billion metric tons). For comparison, Siegenthaler and Sarmiento estimate the total atmospheric carbon pool at 750 Pg. Schuur and coworkers estimate that up to 100 Pg of permafrost carbon could be released as CO_2 to the atmosphere by 2100, assuming current warming trends. This will significantly accelerate global warming.

In the tropics, most computer models predict that global warming will result in less rainfall in the Amazon. A 2°C rise in global temperature would see a 20% to 40% die-off in Amazon forests over 100 years. A 4°C rise in temperature, now held most probable by the year 2100, would kill 85% of the Amazon rain forest. This would in itself contribute to further global warming, by changing the Amazon from a carbon sink in which trees absorb carbon dioxide into a carbon source.

Most computer models, such as those of Peter Good, also show a large temperature increase in the Amazon, comparable to the large increases projected for the polar regions. Coupled with the associated decrease in rainfall, this will spell the end of the Amazon rain forest. The Amazon is the world center of porcupine diversity. Six of the 14 species of South American porcupines are associated with the Amazon.

The effects of global warming on the other porcupine species of the world are more difficult to gauge. Their fate will depend on the fate of their forests. The species with the best outlooks are the crested porcupines (*Hystrix cristata*, *H. indica*, *H. africaeaustralis*), which have broad habitat compatibilities and can live in savanna as well as forest ecosystems. Also favored will be the North American porcupine, which will find northern forests growing in regions of present-day tundra and ice. But for porcupines of the tropical rain forests, the outlook is uniformly grim.

Why do people hunt and eat porcupines?

The porcupine species most often hunted for food are the Old World porcupines of genera *Hystrix* and *Atherurus* whose meat is highly prized. In many African and Asiatic countries, the wild animals killed by hunters find their way to markets as bush meat. Bush meat is perceived as a healthful

meat compared with farm or industrial meat and commands a price premium. The North American porcupine, *Erethizon dorsatum*, is also widely hunted (for "sport"), but seldom eaten nowadays. (As noted in chapter 9, "Is it safe to eat porcupines?" earlier Native Americans did cook and eat porcupines.) Its habit of taking refuge by climbing into a tree makes it an easy target.

Both *Atherurus* and *Hystrix* are sizable animals, providing substantial reward to the hunter. With *Hystrix*, there is the added rationalization that the animal is a pest that raids gardens and agricultural crops. Only in Italy is the crested porcupine (*H. cristata*) protected; there, crested porcupines live in wild areas and abandoned farmland, so the agricultural rationale does not apply. Nevertheless, its legal protection is loosely enforced, and the animal continues to be widely hunted, often with dogs. Italians love the taste of crested porcupine.

In Africa and Asia, the animals are frequently hunted by setting snares. Besides the attraction of their meat, crested porcupines are also hunted for their quills, which have a market as wildlife curios and are used in lampshades, jewelry, picture frames, coasters, and fishermen's floats. But unlike the North American porcupines, which are killed and left to rot, the African and Asian porcupines find their way to the table.

A porcupine recipe from Uganda:

- Do not skin as the skin is the tastiest part of the animal. It is thick and tastes like crackling.
- Pluck out all the large quills.
- Place in boiling water, then scrape off remaining body hair and bristles.
- Remove feet, head, entrails.
- Carefully remove the scent glands (perineal glands) that will taint the meat.
- Stuff with rice, fruits, stuffing, then leave in refrigerator overnight.
- Grease outside of the skin.
- Bake in oven till golden brown and cooked.

A recipe from Thailand suggests that porcupine is best in curry or barbecued with lots of garlic, pepper, and salt. A little vegetable oil should be used when barbecuing. The meat is described as delicious, similar to duck but crunchy and with more flavor. This spirit is echoed in a recipe from Kerala, India, which substitutes for Thai curry a fiery Indian curry base.

While serious market hunting is restricted to the Old World porcupines, a number of South American porcupine species may also be targeted. A February 2012 article in the Brazilian paper *Globo Bahia* recounts a narrow escape by a thin-spined porcupine (*Chaetomys subspinosus*). A bus conductor named Aílton Sampaio saw a group of boys walking past his house,

A North American porcupine shot by a hunter lies in the snow, untouched after the killing.

leading the porcupine with a rope tied around its neck. When asked what they planned to do with the porcupine, the boys replied they were taking it to someone who would kill it so they could eat it. Mr. Sampaio offered the boys 20 *reals* (about $11) for the porcupine, an offer they accepted.

Since the thin-spined porcupine is a protected species in Brazil, Mr. Sampaio got in touch with the Environmental Police, who took the animal to a screening center for wild animals. Mr. Sampaio observed that because of the continuing deforestation in this area of the Atlantic Forest, wild animals—not only porcupines, but also boa constrictors, anacondas, and giant anteaters—often appear in urban areas.

Is there a hunting season for porcupines?

In the United States and Canada, the porcupine is not considered a game animal; hence, most states and provinces do not establish hunting seasons, and the animal can be hunted at any time. However, most states require a valid hunting or trapping license in order to hunt or trap wildlife.

In practical terms, North American porcupines are almost invisible in the summer, when canopy foliage shields them from view. Hunting is therefore generally restricted to the leaf-free season, when porcupines can be seen in trees or snow-tracked to their dens. In coniferous evergreen forests, there is little change in visibility between summer and winter.

Besides the lack of protection, the absence of game laws for porcupines has a further unfortunate effect: they leave it an understudied wildlife

species. The bulk of wildlife studies are carried out by state or provincial fish and wildlife departments, whose budgets are heavily dependent on income from hunting license fees. Because the porcupine does not generate income from such fees, the animal is rarely studied, and its biology is less well understood than the biology of deer, bear, wild turkey, or any of the protected species.

For porcupine species outside North America, only two enjoy current protection: the Brazilian thin-spined porcupine (*Chaetomys subspinosus*) and the Italian population of crested porcupine (*Hystrix cristata*).

What can I do to help porcupines?

For all porcupines, the most fundamental need is habitat. For the thin-spined porcupine of Brazil, habitat loss has reached a critical stage, reducing porcupine numbers to the point where for many years the animals had been feared extinct. Providing habitat, whether in Brazil or the United States or anywhere else in the world, is seldom within the power of individuals. While habitat destruction is primarily the work of individuals and commercial entities, the same groups are seldom effective in habitat conservation. Habitat can be most realistically conserved by the state, with the enforcement of nature-conservation laws that flow from an enlightened society. In the broader perspective, a society that protects its wilderness is protecting itself, through ecosystem services such as flood control, climate amelioration, clean air, and clean water.

Beyond wilderness protection, what can individuals do to help porcupines? In the United States, a major cause of porcupine mortality is roadkill accidents in the early spring, when porcupines venture onto roads seeking residual road salt. (They don't lick the road surface but chew salt-impregnated deadwood along the roadsides.) The sites of such roadkills are as predictable as the sites of deer crossings:

- The highway is salted in winter.
- The highway runs through woods that support porcupines.
- The highway offers few alternative sodium sources such as farmyards or vacation cabins.

In a quixotic attempt to reduce porcupine roadkills in one such area, I have driven down a 4-mile stretch of highway in the spring, throwing out pieces of plywood into the woods away from the highway. The process is not as simple as it sounds. The car has to be moving slowly. The pieces of plywood should be no larger than the size of a dinner plate and at least ½ inch (1 cm) thick. Thinner plywood does not travel far and can curve back in flight to land on the highway.

Plywood is a sodium source that holds its sodium during the spring rains. This is important because more typical sodium salts are quickly leached into the groundwater by rain and snow. I started the process in April 2009 and have repeated it multiple times from 2009 to 2011. Did it work? Here are the number of road-killed porcupines per year along the highway where I "planted" the pieces of plywood:

2005: 2
2006: 4
2007: 8
2008: 3
2009: 2
2010: 1
2011: 1

Although the trend looks favorable, the natural variability of roadkills is too large and the time span of the experiment too short to reach a firm conclusion.

Another resource that is often limiting for North American porcupines is winter den sites. Preferred den sites are natural caves or deep rock crevices: these porcupines do not dig their own dens. Porcupines also use hollow trees and logs. Over the years, I have tried to construct two artificial porcupine dens—a cave-type den built of brick, fieldstone, and soil, and a hollow-log imitation constructed of 12-inch-diameter plastic culvert. The dens were substantial and took considerable effort to construct, but neither den attracted porcupine winter residents.

My two artificial dens did not go empty for lack of porcupines. In the winter of 2010, instead of my brick and stone cave or the plastic culvert, a young porcupine chose a seemingly inferior den some 500 feet (ca. 160 m) equidistant from my creations: the hollow base of an old apple tree. While my culvert den stayed empty, a study by Dessa Montgomery found culverts were the most common den type used by her Texas porcupines. Whereas we have learned to design artificial housing for songbirds, bats, and honeybees, the design of porcupine housing requires further study.

Finally, it is worth remembering that all North American porcupines are starving in late winter and early spring, before buds have begun to swell or leaves have begun to emerge. If during this time you pass an active porcupine den or see a porcupine up in a tree, a red delicious apple left at the entrance to the den or the base of the tree will be eagerly accepted.

Chapter 11

Porcupines in Stories and Literature

What roles do porcupines play in religion and mythology?

The North American porcupine appeared frequently in the mythology of the Woodland Indians. It was the master of winter and had a benevolent, grandfatherly relationship with the woodland tribes. The anthropologist Claude Lévi-Strauss describes a cultural transformation when a woodland tribe, the Arapaho, left their woodland environment in centuries before the European settlement and moved far west to the Great Plains, where they reside today. The tribal affinities of the Arapaho are shown by their language, which is related to the Algonkian languages of tribes such as the Micmac, the Mohicans, the Montagnais, Ojibwe, and Menominee.

Lévi-Strauss notes that the porcupine was rare or absent in the plains where the Arapaho settled. To obtain quills in their new environment, they had to trade with the northern tribes or undertake long hunting expeditions of their own in foreign territory. Perhaps as a consequence, Arapaho quillwork ranks among the finest in North America, and Arapaho art was imbued with a rare mysticism. Before the women undertook such work, they fasted and prayed for supernatural help.

One Arapaho myth describes a quarrel between the brothers Sun and Moon. They discuss what kind of wife each would like to marry. Which would be better—a frog or a human girl? Moon prefers the latter and transforms himself into a porcupine to entice an Indian girl. Coveting the porcupine's quills, she climbs higher and higher in an ever-growing tree the porcupine pretends to take refuge in. By this ruse the porcupine succeeds in luring her into the sky, where he resumes his human form and marries her.

Arapaho mythology transforms the porcupine from a land-dwelling animal, master of the cold and snow, into a sky dweller responsible for biological periodicity. The Moon's wife becomes the first of her sex to have regular menses and to have guaranteed a normal delivery in childbirth. According to Lévi-Strauss, these shifts in the mythological capital of the porcupine proceed from an inarticulate wish to maintain the coherent relationships conceived by the Arapaho in their previous (eastern woodland) environment.

Another kind of transformation of the porcupine myth is shown in the thought of Sigmund Freud. When Freud left Nazi-occupied Vienna for London in 1938, he brought with him his collection of art and antiquities that had stood on his desk at Berggasse 19. Amid small sculptures such as a Greek Eros, an Egyptian Isis, and a Roman bronze Athena, there stood a metal statue of a North American porcupine.

How did the porcupine fit in with Eros, Isis, and Athena? Freud believed that the most effective way to prevent anxiety in the face of an important task was to invent another task and concentrate on it—for example, to catch sight of a wild porcupine. "To find one's porcupine" became a code phrase for Freud. The porcupine statue was a gift to Freud from Dr. G. Stanley Hall on the occasion of Freud's only visit to America, in 1909, when he delivered the Clark lectures. According to one account, Freud claimed he was going to America to catch sight of a wild porcupine *and* to deliver some lectures. The joking remark was meant to deflect anxiety about the lectures.

Dr. Deborah Ann Luepnitz, who has described Freud's porcupine fascination, recalls a fable of porcupines as told by the philosopher Arthur Schopenhauer: A troop of porcupines is milling about on a cold winter's day. In order to keep from freezing, they move closer to each other. Just as they are close enough to feel a neighbor's body warmth, they begin to poke each other with their quills. They spread out, lose the advantages of close contact, and begin to shiver. This sends them back together again, in a cycle of trying to find a comfortable distance between painful proximity and frozen separation.

For Freud, this was a lesson in boundaries: "No one can tolerate a too intimate approach to his neighbor." Freud wrote that the evidence of psychoanalysis shows that almost every intimate relation between two people that lasts for some time—marriage, friendship, parent-child relations—contains a sediment of feelings of aversion and hostility, which escapes perception only as a result of repression. We struggle on a daily basis to balance privacy and community, concern for self and others, sexual union and a space of our own.

Are there porcupines in fables and folk tales?

Just as porcupines are found across the world, porcupine tales abound in many languages and many cultures. The folk tales reflect the world views and cultural priorities of the storytellers. One of the oldest porcupine fables is told by Aesop, the Greek storyteller from the sixth century BC. Aesop is credited with hundreds of fables that survive to this day. Here is his story about a porcupine and some moles:

> It was getting cold, and a porcupine was looking for a home. He found a wonderful cave, but saw it was already occupied by a family of moles. "Would you mind if I shared your cave for the winter?" he asked. The generous moles agreed, and the porcupine crawled in. But the cave was small, and every time the porcupine moved, he scratched the moles with his sharp quills. Finally they could not endure the pain any more and spoke to the porcupine: "Pray leave. Let us have our cave for ourselves again." But the porcupine did not want to hear this. "Oh no! This cave suits me very well. If you are unhappy, why don't *you* leave?"
>
> The poor moles had to accept their unwelcome guest. Too late they realized that it is important to get to know one's guest before inviting him into the house.

For a porcupine tale from the New World, here is a Menominee tale of how the porcupine got its quills:

> Long ago when the first porcupine was placed on the earth by the Great Spirit, he had no quills. Porcupine was a gift to the Menominee Tribe, and he was given a beautiful coat of fur. Porcupine's beauty made the other animals jealous. Every day the animals would come to Porcupine and tell him how much they wished their fur looked like his. Now Porcupine knew he was beautiful, but he didn't pay any attention to the other animals. As time went by and every day he heard how wonderful he looked, he decided to see for himself. While Porcupine was taking his morning walk, he stopped by the stream to admire his fur. Now the Great Spirit noticed Porcupine gazing at himself in the stream. The Great Spirit watched Porcupine for ten moons as he sat by the clear water admiring his own beauty. The Great Spirit had a code of rewards and punishments for every creature; the time had now come to punish Porcupine. The Great Spirit decided to take away Porcupine's beautiful fur and cover his body with ugly, sharp quills. Porcupine wears his coat of quills yet today. This is why he hides during the day and only comes out at night.

Another New World story, told in many versions, focuses on the porcupine's mastery of winter. Here, I paraphrase a Chippewa version told by Louise Jean Walker:

Winter was approaching, and beaver was working hard to get ready. He prepared a large cache of willow twigs and branches and stored it in the pond near his lodge. Porcupine, who had made no preparations of his own, found the cache and stole it. Enraged by the theft, beaver called on his people to find porcupine and punish him.

Porcupine, sitting in the top of a tall tree, felt himself safe from the beavers below. But the beavers, using their powerful teeth, felled the tree and captured the porcupine. They took him to a barren island and left him to starve.

Getting weak from lack of food, porcupine called out to the North Wind. Howling, the wind arrived in a swirl of white, and froze the sea solid. Porcupine walked back to the mainland and enlisted his fellow porcupines to capture beaver and punish him. Surprising him on the land, they captured him and carried him to the top of a tall tree. There they left him to the same fate he had wished on their brother. But when they looked next morning, both the tree and the beaver were gone. During the night, the beaver had used his strong teeth to chew the tree down to the stump, leaving behind only a pile of wood chips.

Edna Mason Kaula provides another porcupine folk tale from the Baluba tribes of Central Africa:

Porcupine wanted to be friends with elephant and hippo, but the big animals showed no respect for someone as small as a porcupine. They told him he was a creature of no importance.

Then porcupine had an idea. He found a long, stout rope and carried it to the elephant.

"You may be bigger than I am," he told the elephant, "but I am stronger. Take this end of the rope and I will take the other. When I give the rope a shake, start pulling. Then we will see who is stronger."

Elephant picked up the rope, wrapped it around his trunk, and waited for the signal. Porcupine then ran to the river, found hippopotamus, and delivered the same challenge. Hippo picked up the other end of the rope in his teeth and waited. Porcupine moved into thick bush where the two giants could not see him, and gave the rope a shake. Now began a mighty tug of war that lasted all day without a clear result. Then porcupine cut the rope with a sharp quill, sending the two contestants falling backward.

Porcupine rushed to see the elephant, who had bloodied his trunk and sprained a leg. "Friend porcupine," elephant cried out. "You have proved that despite your size, you are my equal in strength. Let us be friends!"

Porcupine next rushed to the hippo who was massaging his gum where the rope had loosened a tooth.

"Friend porcupine," rumbled the hippo. "I am worn out struggling with you while you don't have a quill out of place. You are stronger than you look. Let us be friends!"

And forever after, porcupine was happy to know that despite his small size, the big animals respected him.

And for a story about the Indian crested porcupine, here is "The Porcupine Daughter" from Gujarat, as recounted in Beck's collection of Indian folktales:

Long ago there lived a jamindar (a rich landlord). He had so much land he could not cultivate it all, so in exchange for a half share of the harvest, he gave some of his land to a Kunabi (member of a caste that practiced farming). The Kunabi tilled and watered the land, and fertilized it with cow dung, and every year his crop grew larger and he became rich. Now the jamindar began to regret the arrangement, thinking he could cultivate the land himself. He went to the Kunabi, declared the Kunabi was now rich, and should return the land to the jamindar.

The Kunabi agreed, on condition that the land itself should decide whom it belonged to. The two should go to the land at night and call out. Whichever man's call was answered would become the legal owner of the land. The jamindar agreed, and the two men put the agreement in writing, with witnesses to observe the signing.

But the Kunabi devised a scheme to fool the jamindar. He went to his daughter and proposed that a pit be dug in the field in which the daughter would hide, with air holes for breathing. He explained the jamindar would call first, to which the daughter would not answer. When the Kunabi called, the daughter should call back, "Oh, oh!" The daughter, faithful to her father, agreed.

On the appointed night, the two men went at night to the edge of the land, with villagers along to witness the test. The jamindar called first, but there was no reply. Then the Kunabi called, and the land answered "Oh, oh!" Dejected, the jamindar left, and the Kunabi was acclaimed as the new owner of the field. The villagers dispersed.

At midnight, the Kunabi returned to open the pit and release his daughter. But when the cover of the hole was removed, the Kunabi was shocked to find his daughter gone. Left in the bottom of the pit was a porcupine. "Where is my daughter?" he cried. Seeing the father distraught, the porcupine answered, "Dear father, you have cheated our mother land, and I have been cursed to become a porcupine. I must now spend my life with four legs and quills."

The father sobbed and said, "Dear daughter, henceforth let no Kunabi

beat you or kill you. You must be allowed to eat sugar cane, beans, peas, and millets from the fields just as men eat them."

To this day, porcupines are not hunted or killed in Gujarat. And their cry is said to sound just like the weeping of a human child.

The thick-spined porcupine, *Hystrix crassispinis*, plays a key role in a fairy tale from Indonesia, as recounted by Harold Courlander. The hero of the story is Kantchil, the mouse deer. It stands only a foot high but compensates by having the sharpest wit of all the animals.

Once upon a time, tigers ruled the island of Java. Their tenure was uneventful until a great famine broke out. As the tigers starved, the tiger king gathered a grand council of his advisors. They concluded that the only way out was to invade the island of Borneo, where they would find food and force the inhabitants to pay tribute.

The tiger king appointed three messengers to meet the king of Borneo and deliver an ultimatum: "Send us food and gold, or we shall come with an army to conquer you!" And to impress the king of Borneo, the tiger king plucked the largest whisker from his face and sent it along as proof of his strength.

The tiger messengers crossed the sea of Java, landed on Borneo, and began to search for its king. But search as they might, they could not find any trace of the king or his people, who had heard of the arrival of the tigers and had gone to hide in the woods. Finally the messengers came upon Kantchil, the mouse deer, who awaited them in a little clearing in the woods. The tigers demanded he bring them to the king of Borneo, so they could deliver their ultimatum and show the large whisker. Kantchil replied that his king was hunting in the forest, but promised to find him and convey the message and deliver the whisker, which he carried away respectfully while the tigers waited.

Kantchil went to the cave of the porcupine Landak and asked him for one of his quills. The porcupine pulled a quill from his back and gave it to Kantchil, who then returned to the clearing where the tigers were waiting.

He told the tigers he had found his king resting after the hunt, while his servants sharpened his claws by grinding them between two mountains. His message to the tiger king was that his soldiers were tired of their peaceful lives on Borneo and burned to go to war. Kantchil told the tigers that to show his readiness, the king of Borneo had plucked a whisker from his face and was sending it to the tiger king. With that, he produced the porcupine quill, which was 20 times thicker than the tiger king's whisker.

When the messengers returned to Java with the reply message and the quill, the tigers abandoned their plans. And that is why there are no tigers on Borneo today.

What role do porcupines play in native cultures?

North America. Unquestionably, the strongest human-porcupine linkage existed between Native Americans and the North American porcupine. As mentioned before, the linkage was so strong that a number of northeastern tribes were known as the Porcupine Indians. The connection was twofold. First, the porcupine represented an emergency food supply to the woodland Indians, who did not have an agricultural economy but lived by hunting, fishing, and gathering of fruits and tubers. During early winter, when these subsistence modes failed, only the porcupine and beaver remained as accessible game.

Second, the porcupine provided the raw materials for quillwork, a uniquely Native American art form. Quills were collected, sorted by size, and boiled in vegetable dyes that produced vivid reds, yellows, blues, and black. The dyes came from a variety of roots, leaves, tree bark, lichens, and fungi. Mordants (bonding agents) were commonly added to make the colors durable and more intense. Gathering of the dyes required a sophisticated knowledge of local botany.

The dyed quills were then tightly fixed in a leather or birch-bark ground, after fine holes had been punched by a bone awl. Even small articles like purses and tobacco pouches required an astonishing amount of work. Because the product was beautiful and difficult to make, it served as a universal medium of exchange before the introduction of wampum, a European product.

These linkages guaranteed a special position for the porcupine. It was not hunted unless absolutely necessary, and its remains were treated with respect. The porcupine also found its way into native myths, folk tales, and clan designations.

South America. Among the indigenous people of Bolivia, porcupines continue to appear in shamanism. The species used are *Coendou prehensilis* and *C. bicolor*; both have long prehensile tails with quills at the proximal end. In Bolivia, such folk medicine is practiced in broad daylight in the middle of the town. The large city of El Alto, sister city of La Paz, has its own shamanistic market patronized by the Aymara, the indigenous group of this region.

Market patrons include farmers hoping for a better crop, truckers hoping for an accident-free year, urban dwellers seeking help with "love, travel, marriage, health, legal problems, making lost things appear, duty inspections, exams at the teacher's college." Market vendors provide the materials needed to perform the magic services: fetuses of llamas and deer, tails of porcupines, leaves of coca, and other potent ingredients.

When these have been purchased, the customer engages a *yatiri*, the person who conducts the service, or *misa*, in which the magical items are stacked on a plate, then incinerated on a bed of coals. The yatiri splashes alcohol on the coals to make the flames leap up and chants appropriate verse. At the end of the ceremony, the unburned materials are collected and buried in the earth, the source of all dispensation and mother of all creatures.

In eastern Brazil, Santos and coworkers, who visited 292 locations, report that among the impoverished communities of southern Bahia province, the quills of the Bahia porcupine (*Coendou insidiosus*) are believed to have medicinal and magic properties. Smoke from burned quills is prescribed for women with difficult childbirth. The smoke, generated by inserting a quill into a cigarette, is also thought to be a remedy for asthma or toothache. Alternatively, the medicine may be administered as an infusion made from quill ashes mixed with bee stings and birds' nests.

People in the area believe that quills are alive and should be kept in sealed jars to prevent escape and burrowing into the heart. They consider quills to be either male or female, with the males longer. A male-female pair may reproduce if kept in a jar with raw cotton. When people are unable to raise their own quills, they may purchase them in village markets.

Africa. In Kenya and Malawi, the meat of the Cape porcupine (*Hystrix africaeaustralis*) is considered to be a strong aphrodisiac. One recipe starts with roasted porcupine meat. After roasting, the meat is mixed with oil and reheated. When the oil has cooled, the mixture is then rubbed over the skin, after which the prospective lover walks to the local bazaar to enjoy the reactions of the opposite sex.

Europe. The crested porcupine, *Hystrix cristata*, plays a leading role in an annual Italian festival in Siena called the Palio. The Palio climaxes with a horse race run in the Piazza del Campo, in the center of the medieval town. The race is a colorful event, first run in 1701 and repeated annually. The race is preceded by a pageant in which each of the 17 districts of Siena participates, displaying the traditional colors and images of its animal patron. One of these is the porcupine (*Istrice*). Some others are the ram, the dragon, the caterpillar, and the eagle. The heraldic image of the porcupine wears a golden crown and carries two red flowers.

The Palio was initially created to find a harmless channel for the dangerous strife between the districts of Siena. Now, instead of swords and daggers, the young men spend energy on a horse race, oratory, and a parade in brilliant costumes.

Southeast Asia. In Indonesia and parts of China, porcupines are connected with bizarre objects called *bezoars*. Bezoars may be thought of as the mammalian equivalents of pearls. A bezoar starts as a hairball or fibrous mass in the body of the porcupine, usually the stomach. The irritant becomes encapsulated in layers of bile steroids to form the bezoar. Bezoars are found in many animals and on all continents, but in Borneo and surrounding regions, the most prized bezoars come from porcupines (*Hystrix crassispinis*, *H. pumila*, *H. javanica*).

Bezoars are rare and therefore expensive. They are thought to convey immunity to poisons. If a person suspects he has been poisoned, he might lick a bezoar or drink it in a water suspension to counteract the poison. In parts of China, bezoars are valued for their supposed aphrodisiac effect, achieved by drinking a suspension or by wearing the bezoar around the neck. This belief comes from the observation that a porcupine's quills spring instantly erect.

In nineteenth-century Sri Lanka and India, quills of the Indian crested porcupine were used in a type of quillwork. Unlike the quillwork of North America, the quills of the Indian crested porcupine were not dyed or incorporated into deerskin or tree bark. Instead, the large quills were sectioned, sorted by natural color, and used as a veneer on jewelry boxes, lap desks, and the like. Such artifacts remain a staple in Anglo-Indian antique shops.

How are porcupines featured in poetry and literature?

Porcupines make many appearances in children's literature. The animal is so original and so universally recognizable that one alphabet for French children goes

A—Arbre (tree)
B—Bouteille (bottle)
C—Canard (duck) . . .
P—Porc-epic (porcupine) . . .

There are no porcupines in France, yet French children recognize the animal instantly.

Some children's books are excursions in natural history. Others do what folk tales have always done: get inside the mind of an animal and weave a story. A fine example of this is Van de Wetering's "Hugh Pine," the story of a Maine porcupine who learns to talk human and enlists the aid of the town's postmaster to stop the roadkilling that is erasing Hugh's friends and family. The solution? Erect a pair of Porcupine Crossing signs! The sensitive drawings of Lynn Munsinger enhance this little book.

The porcupine also appears in children's poetry, as in this delightful verse of Hilaire Belloc (1870–1953) entitled "The Porcupine." (Note that in the opinion of Belloc, a tupto-philist is one who loves to spank.)

What! Would you slap the Porcupine?
Unhappy child—desist!
Alas! That any friend of mine
Should turn Tupto-philist!

To strike the meanest and the least
Of creatures is a sin;
How much more bad to beat a beast
With prickles on its skin!

Shakespeare mentions the porcupine in act 1, scene 5, of *Hamlet*, but only as a figure of speech:

Ghost: I could a tale unfold whose lightest word
Would harrow up thy soul, freeze thy young blood,
Make thy two eyes, like stars, start from their spheres,
Thy knotted and combined locks to part
And each particular hair to stand on end,
Like quills upon the fretful porpentine.

In much of adult literature, the porcupine plays the same role it played for Schopenhauer and Freud: it serves as a symbol. Such is the position the porcupine holds in Julian Barnes's 2000 novel, *The Porcupine*. The action is set in an unnamed East European country at the time of the 1991 Soviet collapse. The new government puts the former dictator on trial, and a friend warns the prosecutor to be careful. The prosecutor answers: "Careful? Of course I shall be careful. Look—I am wearing my porcupine gloves!" That is the book's only explicit reference to porcupines. But as the trial unfolds, the prosecutor discovers his antagonist is defending himself with unexpected skill—just like a porcupine!

Two other works also entitled *The Porcupine*—Edwin Arlington Robinson's 1916 play and Meg Tilly's 2007 novel—create their titles from the same symbolic cloth. No actual porcupines inhabit these works.

A porcupine that is again symbolic, but also takes on a deeper dimensionality, appears in the fable "The Wolf and the Porcupine: In Answer to the Argument against a Standing Army," by Thomas Brown (1663–1704). In Britain, a small standing army was first established by Charles II following the Restoration. Opponents feared the army would be used to suppress the wishes of Parliament. Brown was a Royalist. Here, the wolf speaks first, noting that the war is over, and suggesting the porcupine disarm:

The plains a pleasing prospect yield,
No fire, nor desolation;
While plenty reigns in every field,
And trade restores the nation.
Yet you your quills erected wear,
And tho' none seeks to harm ye,
In time of peace about you bear,
Methinks a standing army.
Friend, quoth the porcupine, 'tis true,
The war's at length decided.
But 'gainst such tricking blades as you,
'Tis good to be provided.

We meet a living porcupine in Henry Wadsworth Longfellow's "Song of Hiawatha," where, to preserve the poem's meter, its name is changed to Hedgehog:

From a hollow tree the Hedgehog
With his sleepy eyes looked at him,
Shot his shining quills, like arrows,
Saying with a drowsy murmur,
Through the tangle of his whiskers,
"Take my quills, O Hiawatha!"

A tables-turned porcupine shows up in Ogden Nash:

Any hound a porcupine nudges
Can't be blamed for holding grudges.
I knew one hound that laughed all winter
At a porcupine that sat on a splinter!

A porcupine baby is often on display in Louise Erdrich's appealing coming-of-age tale *Porcupine Year*. The book is a gripping recreation of the events of 1852, when the United States government forced the Ojibwes and other tribes from their native lands in the upper Midwest to make way for European settlers. We follow the adventures of a 14-year-old girl and her family in a life-and-death encounter with a wilderness on which they depend for survival. A baby porcupine travels with them, but it functions mostly as headgear for the girl's brother, in whose hair it likes to ride.

To meet porcupines with a self-awareness and life force of their own, we have to go to the works of Galway Kinnell, D. H. Lawrence, Linda Hogan, and others. These are writers who are rooted in the literary tradition but who try to reach into the consciousness and life experience of animals we share the world with. Kinnell's poem "The Porcupine" is divided into three

sections. It begins with a description of the animal in its daily rhythms, and shows an accurate naturalist's eye. Kinnell goes on to marvel at the animal's salt drive, the behavior that brings it into fatal conflict with humans.

The second section of the poem begins with a murder: a farmer shoots a porcupine caught dozing in his apple tree. As the porcupine falls, it performs the biologically improbable act of snagging its intestines on a branch and leaving them behind in the tree like an unwinding thread on a spool.

In the poem's third section, Kinnell returns as avenger and witness. He notes darkly that the Avesta, the holy book of the Zoroasterians, puts porcupine killers into hell for nine generations. Then he pictures himself as the murdered porcupine, a "Saint Sebastian of the scared heart." In this act of sympathetic imagination, the author tries to do for the porcupine what humans insist on doing for their own kind: bring murder to light.

D. H. Lawrence, in his essay "Reflections on the Death of a Porcupine," likewise begins with a naturalist's bright gaze at a porcupine. But at the beginning, he plants a seed: it must be killed:

> Everyone says, porcupines should be killed; the Indians, Mexicans, Americans all say the same. At full moon a month ago, when I went down the long clearing in the brilliant moonlight, through the poor dry herbage a big porcupine began to waddle away from me, towards the trees and the darkness. The animal had raised all its hairs and bristles, so that by the light of the moon it seemed to have a tall, swaying, moonlit aureole arching its back as it went. That seemed curiously fearsome, as if the animal were emitting itself demon-like on the air.

By the end of the account, the animal is dead, and Lawrence is explaining why:

> As far as experience goes, that life-species is the highest which can devour, or destroy, or subjugate every other life-species against which it is pitted in contest.
>
> This is a law. There is no escaping this law. Anyone, or any race, trying to escape it, will fall a victim: it will fall into subjugation.

Lawrence goes on:

> Freedom lies in the honourable yielding towards the new flame, and the honourable mastery of that which shall be new, over that which must yield. As I master my horses, which are in a lower cycle of existence. And they, they are relieved and *happy* to serve. If I turn them loose into the mountain ranges, to run wild till they die, the thrill of real happiness is gone out of their lives.

Lawrence's "Reflections on the Death of a Porcupine" was written in 1925. Barely 10 years later, the ideas expressed in the reflections were widely circulated in Europe, and in a political context. By 1945, those ideas had run their course.

Here is a very different account of a porcupine's death. The death is a natural one, not inflicted by human hand, and in the death there is a biological resurrection. The author is Linda Hogan in her story "The Porcupine." The porcupine she describes is

> torn and lame and her undignified quills are broken on one side, as if she had slept them tangled. She hobbles and limps away from her many batterings. She wears her history, dark and spiney, and there is a light in her, a fire around the dreary sharp halo of quills. . . .
>
> One evening I find her lying dead beside the road. She has come closer to the house than usual. The thick hairs are visible among the broken quills. I look closely at her, the clean long gaze that death permits us. Her face is sweet and dark, her inner light replaced by the light of sky. The drifting clouds are in her eyes.
>
> As for me, I have a choice between honoring that dark life I've seen so many years moving in the junipers, or of walking away and going on with my own human busyness. There is always that choice for humans.

Following its death, the porcupine is consumed by a swarm of tiny carrion-feeders, and Hogan reflects:

> In that crossing over, that swallowing, the battle of life with life, the porcupine lives on. It lives on in the buzzing of flies and the ants with their organized lives. In its transformation, life continues. My life too, which stopped only for a small moment in history, in the great turning over of the world.

Kinnell, Lawrence, and Hogan are all reflecting on the death of a porcupine, and each brings his or her own moral dimension to the act. For Lawrence, the death of a porcupine is an expression of natural law. The porcupine must be subjugated and killed because the human is the higher species. For Kinnell, the death is a murder and his poem an act of justice. For Hogan, whose porcupine dies naturally, the death is woven into the cycles of nature, and in this sense it is not a death but a passage into new life.

And finally, some blues by Howard L. Kaplan, who reflects on the porcupine not in terms of moral values, but as an animal with interesting life experiences and biological relationships. Kaplan is a Toronto song writer and psychology Ph.D. who has explored many topics in song, including

frogs. Here he sings, in a scholarly way, about the North American porcupine. And because of its scholarly nature, the song ends with a reference!

The Ex-Arboureal Porcupine Blues
By Howard Kaplan

Here's the situation I want you to consider if you please:
Now, it seems that porcupines are accidentally falling out of trees.

It's been happening for a while, as a search through museums has revealed:
One finds lots of skeletons with evidence of fractures that have healed.

One might hypothesize falling would make them ill
Through infection secondary to the self-impalement on a quill.

Well, that's not the case, for the lubricant that helps a quill glide
Through the flesh of an attacker is also a bactericide.

Now, the fisher is a weasel with a mighty fine coat of fur
Who has been extirpated from most places he used to occur.

The quick, clever fisher is an animal that's able to dine
Upon the flesh of the slow but prickly porcupine.

He goes for the face, which is toothy but is lacking protection,
Circling to avoid the tail, slashing from the other direction.

The porcupine, exhausted, is flipped on its back,
Leaving the unprotected belly open to attack.

When thin branches tempt a porcupine with buds or fruit,
Ex-arbouration can be the consequence of their pursuit.

It's safer to nip off the twigs and eat the treats out of hand,
Which tends to leave a lot of stunted, funny-looking trees on the land.

And those who are managing a forest for its lumber or a park
Don't like to have too many porcupines a-nibbling at the bark.

So, the fisher has been introduced again to play his old role
In keeping the tree-nibbling porcupine under control.

I've a major reference to cite for you before I close:
The North American Porcupine, by Uldis Roze.

What king used the porcupine in his royal seal?

The king was Louis XII of France (1462–1515), who ascended to the throne in 1498. Prior to assuming the crown, Louis XII had been the duke

of Orleans, and the porcupine he incorporated into his royal seal was the porcupine of Orleans, where it had served as the emblem of a knightly order. The motto of the House of Orleans was *cominus et eminus*, or "near and far." This referred to the supposed ability of the porcupine to shoot its quills against a distant enemy as well as defend itself at close range with its phalanx of body quills.

Louis XII led a series of disastrous military campaigns against the duchies of Milan and Naples. Perhaps as a result, his successors soon abandoned the porcupine symbolism. Nevertheless, Louis remained a popular king. Unlike his eighteenth-century successors, he did not resort to massive taxation to pay for his wars. He reformed the legal system and held the country together. His grateful subjects called him Father of the People.

What place names feature the porcupine?

The names we give our streets, cities, mountains, rivers, and other landmarks say something about our sense of values and cultural focus. Thus, the east-west streets in Chicago's center are named after six early U.S. presidents, from Washington to Van Buren. The radiating avenues of Washington, D.C., are named for eight states, only one of which, Georgia, is found in the South. Contrast these with the names of 20 large lakes of Saskatchewan, all of which are named for local plants and animals (Little Bear, White Bear, Swan, Bittern, Birch, Crane, Turtle, Waterhen, etc.). There is even a small Porcupine Lake.

It is a fair guess that the people of Saskatchewan are more attuned to the wildlife and nature around them than were the founding fathers of Chicago or Washington, D.C. As the widespread use of "Porcupine" as a place name suggests, the same empathy with nature holds true across much of North America. The *Atlas of Canada* alone gives 152 place names that include the word "Porcupine" (http://atlas.nrcan.gc.ca/site/english/search), including towns, rivers, lakes, bays, reefs, coves, islands, beaches, mountains, and conservation areas. To these can be added 38 place names based on *Porc-epic*, the French word for "porcupine." It is clear that the North American porcupine is deeply embedded in the consciousness of the human tide surrounding it.

A few of the porcupine place names in the world are given below.

Towns

Porcupine, South Dakota, pop. 407. Located on the Pine Ridge Reservation, north of Wounded Knee; its population is 98 percent Native American.

Porcupine Plain, Saskatchewan, pop. 820. The town is adjacent to Greenwater Lake Provincial Park.

The royal crest of Louis XII of France. The animal is throwing a shower of quills at its enemies, while keeping other quills in reserve as an impregnable defense. The porcupine species pictured is the crested porcupine, *Hystrix cristata*, which does not occur in France. With a poor understanding of porcupine anatomy, the artist placed the porcupine's crest on top of its head, in front of the ears. Photo by Philippa Moore.

Mountains

Porcupine Peak, Alaska, elev. 5,330 feet. In Haines County, north of Glacier Bay National Park.

Porcupine Peak, British Columbia, elev. 9,144 feet. Lat. 51.333, long. –116.717.

Porcupine Peak, Chilliwack Forest, British Columbia, elev. 6,496 feet.

Porcupine Peak, California, elev. 7,550 feet. Near Mt. Eddy. It takes its name from Porcupine Lake, located at the northern foot of the mountain.

Porcupine Peak, Colorado, elev. 11,803 feet. It is part of the White River National Forest and sits within a 13.6-mi^2 roadless area. Animals include bighorn sheep, mountain goat, porcupine, and lynx.

Porcupine Peak, Utah, elev. 8,251 feet. In Morgan County, northeast of Salt Lake City.

Mt. Porcupine, New South Wales, Australia. At 6,270 feet, it is one of the highest peaks on that continent.

Rivers

Porcupine River, Canada and Alaska, 448 miles (721 km) long. The river starts in the Ogilvie Mountains of Yukon Territory and initially flows north, then veers west and flows into the Yukon River at Fort Yukon, Alaska. The river gives its name to the Porcupine caribou herd.

Islands

Porcupine Islands, off Bar Harbor, Maine. The islands are part of Acadia National Park, whose Cadillac Mountain offers a good view of the four small islands. From this vantage point, the islands look

like crouching porcupines, their heads down and facing north. The north faces were scraped bare by the advancing glaciers; the south coasts have high cliffs. Today, the islands are thickly forested and are homes for nesting eagles, ospreys, and seals. There are pocket beaches, accessible by boat.

State and provincial parks

Porcupine Meadows Provincial Park, British Columbia. Located 25 miles (40 km) northwest of the town of Kamlops, BC, the 27-km^2 park contains areas of old-growth forest and undisturbed wetlands that support sandhill cranes.

Porcupine Mountains Wilderness State Park, Michigan. In the northwestern part of Michigan's Upper Peninsula, on the shore of Lake Superior. The park takes its name from the Ojibwe observation that as seen from a canoe in Lake Superior, the adjacent mountains look like crouching porcupines. The mountains are low and rounded, with the highest peak rising only to 1,958 feet. The park contains 92 mi^2 of undeveloped wilderness and the largest virgin hardwood-hemlock forest in the United States There are virtually no roads but 87 miles of hiking trails. These woods, composed of hemlock, maple, basswood, and birch, were the inspiration for Longfellow's famous lines from "Evangeline":

> This is the forest primeval, the murmuring pines and the hemlocks,
> Bearded with moss, and in garments green, indistinct in the twilight.

The park has 20 miles of Lake Superior shoreline and contains some 60 waterfalls. Its animal life includes wolves, bears, eagles, and peregrine falcons. Established in 1945, the park came into being because of a passionate campaign by environmentalists, including Aldo Leopold.

Chapter 12

"Porcupinology"

Who studies porcupines?

Porcupines are studied by mammalogists. Two threads unite most mammalogists: their subject matter (the mammals) and their education (typically a master's or a Ph.D. degree). Achievement of the master's or the doctorate represents the successful completion of an apprenticeship, during which the aspiring mammalogist works under the tutelage of a mentor with a Ph.D. degree. The apprenticeship is successfully concluded by completing a study that meets the criteria of the profession. Most often, the candidate's grasp of the subject is demonstrated by publication in a peer-reviewed scientific journal. The study must represent new knowledge (which implies mastery of the old knowledge), and it must satisfy the standards of proof of the discipline.

This definition of a mammalogist is extremely broad. All aspects of an animal's biology can become the objects of investigation: its evolutionary relationships; its behavior; its social structure; its physiological processes of vision, hearing and smell, heat conservation, water conservation, sodium metabolism, lung capacity, reproductive cycles. There are also the ecological studies of food supply, predator avoidance, parasites, and competitors.

A typical mammalogist will know something about all of these topics or will know where to go to find out more, but very few will be qualified to make creative contributions in all subject areas related to a specific mammal or mammal group. Their expertise will be limited by their training and past experience and by their own temperament. The skills required to study the molecular genetics of an organism are entirely different from skills required to study its mechanisms of heat conservation. This is why

mammalogists are a diverse group, able to see a porcupine (or an antelope or a bobcat) in multiple dimensions and in depth.

On a comparative basis, mammalogy is one of the less expensive sciences in which to work. The Large Hadron Collider, now undergoing startup near Geneva, Switzerland, will cost an estimated 3.2 to 6.4 billion euros ($4.2–$8.4 billion). The cumulative cost of the Hubble space telescope was about $10 billion in 2008, according to C. Markowitz in *USA Today*. The research budgets of all the mammalogists of the world, combined, do not approach these levels.

Yet conducting research in mammalogy is not free. Mammalogists need computers, field stations, animal facilities, lab space, and lab reagents; and they need salaries. These have not always been available in the less-developed countries of the world. But as the signal of a brighter future, there are now more mammalogists working in South America than there are in the United States. All are working to their best ability and publishing in national and international venues.

Which species are best known?

Unquestionably the world's most-studied porcupine is the North American porcupine. Generations of biologists—beginning with Michel Sarrazin, an eighteenth-century French-Canadian naturalist and medical doctor—have studied the animal. A solid layer of knowledge has been accumulated, though many mysteries remain. Some of the areas explored include

- seasonal food preferences and feeding modes
- digestive physiology: the role of the caecum in digestion and sodium storage; the detoxification of plant defense compounds; digestive transit time; the role of the large intestine in water conservation and sodium retention
- thermoregulation and basal metabolic rate
- reproductive physiology and behavior: the seasonality of breeding; guarding behavior; the estrus cycle of female; progesterone levels in pregnancy maintenance; the role of the accessory corpora lutea (the progesterone-producing ovarian structures in pregnancy)
- sodium drive: seasonality, sex differences, sodium sources
- social structure: male-female territoriality, juvenile dispersal, variance in male-female reproductive success
- anatomy: quill structure, erection, and detachment mechanisms; odor-dispersing, warning, and antibiotic properties; arboreal adaptations of limbs and tail; tooth structure and replacement; adaptations for chewing and gnawing; anatomy of reproductive organs

- ecology: roster of parasites; the role of predators in population control; den use; species range

The crested porcupines of the Old World—*Hystrix africaeaustralis*, *H. cristata*, and *H. indica*—are the second best-studied porcupine group, but we know less about their social structures and anatomy than we do about the North American porcupine. Fewer mammalogists have studied this species group, and studies reach back for a shorter period of time.

Which species are least known?

Least known are the porcupines of Central and South America. Only four species—*Coendou prehensilis*, *C. mexicanus*, *C. spinosus* (as *Sphiggurus villosus*), and *Chaetomys subspinosus*—have been followed by radiotelemetry. In a science turnaround, the strongest research effort in this group has focused on the thin-spined porcupine, *Chaetomys subspinosus*, a vulnerable species only recently feared extinct. The work has yielded basic ecological information on this porcupine's food choices, activity budgets, home range and movement, latrine use, mother-infant relationships, and more.

Regrettably, for most of the South American species nothing is known about natural behavior. For some, even the species ranges are unknown. We don't know their population densities or population trends, or how the species are ecologically separated from other porcupines (by feeding mode, food choices, habitat requirements). We don't know whether hybridization is possible between species coexisting in the same area. We don't have any idea about predator pressure or the role of parasites. There is a real danger that some species may be lost before we have learned anything about them.

How do scientists tell porcupine species apart?

At the time of this writing, scientists have named and described 26 species of porcupines (appendix A). To see how this has been accomplished, consider some high points in the historical process. Just four scientists have named and described more than half the species known today:

Carolus Linnaeus, 1707–1778 (6 species)
Ignaz von Olfers, 1793–1871 (3 species)
Frederic Cuvier, 1773–1838 (3 species)
Oldfield Thomas, 1858–1929 (3 species)

Of the six species named by Linnaeus, five are so radically different from each other that there is no question of their uniqueness. These five original Linnaean species —*Atherurus macrourus* (Asian brush-tailed porcupine), *Hystrix brachyura* (Himalayan porcupine), *Hystrix cristata* (crested

porcupine), *Coendou prehensilis* (Brazilian porcupine), and *Erethizon dorsatum* (North American porcupine)—are listed in the 10th edition of Linnaeus's *Systema Naturae* (1758), issued 20 years before his death. (This edition listed 4,400 animal and 7,700 plant species from across the world, and popularized the binomial system of nomenclature, where the first name stands for the genus and groups together related species.)

Thus, the Himalayan porcupine and the crested porcupine are easily differentiated on the basis of body weight and the absence of a conspicuous erectable crest in the Himalayan porcupine. Yet the two porcupines have so many affinities (such as very large quills, relatively large body sizes, and short tails bearing rattle quills) that the two species are thought to be closely related and are grouped into a common genus, *Hystrix*.

A sixth porcupine credited to Linnaeus is *Hystrix indica*, the Indian crested porcupine. This species was not included in the *Systema Naturae*; the Linnaean description was published posthumously in 1792. The Indian crested porcupine is closely related to both the crested porcupine, *H. cristata*, and the Himalayan porcupine, *H. brachyura*; all three are in the genus *Hystrix*. But the differences between *H. indica* and *H. cristata* are more subtle than the differences separating *H. cristata* and *H. brachyura*. One of the differences is the shape of the skull: the *indica* skull is relatively more massive than the skull of *cristata*. Another difference is the color of the crest (dark in *H. indica*, light in *H. cristata*). The sum of such differences added up to a biological configuration that told Linnaeus that the two porcupines represented different species. Perhaps to Linnaeus the observed differences were so small that he delayed recognition of *H. Indica* within his lifetime.

Today, morphological differences between species are treated more rigorously. First, the differences are quantified. Instead of describing one skull as more massive than another, biologists measure and compare specific landmarks of the skull. And to compensate for body-size differences, the measurements may be expressed as ratios. Second, biologists recognize that individuals of a given species are variable. Rather than comparing individual animals, biologists compare larger or smaller groups, noting the range of variation within each group. Thus, Corbet and Jones have shown that *H. indica* and *H. cristata* are easily distinguished on the basis of the length ratios of two skull bones, the frontal and the nasal. But such ranges of variation are useful in making interspecific comparisons only when they do not overlap between species.

The six porcupines described by Linnaeus came from across the world. Linnaeus, who worked at Uppsala in Sweden, did not actually travel to North America or southern Asia to collect his samples. Instead, he sent out collectors to collect plants and animals for him. In addition, his universal fame encouraged people to send him specimens from across the globe.

Linnaeus was most fascinated by plants and animals from the New World. A man with a similar passion was Ignaz von Olfers (1793–1871), a Prussian diplomat and naturalist, who described three additional South American porcupines in 1818: *Chaetomys subspinosus* (thin-spined porcupine), *Coendou nycthemera* (black dwarf porcupine), and *Coendou insidiosus* (Bahia dwarf porcupine).

Olfers also described new South American mice, bats, opossums, and other species. He was able to accomplish this because in 1816, at the age of 23, he had entered the Prussian diplomatic service and had been posted to Brazil. Inspired by his great contemporary Alexander von Humboldt, Olfers prepared himself for his assignment by visiting the Berlin Zoological Museum and carefully studying its South American collection, which included the three porcupine species noted above. In a labor of love, Robert Voss and Renate Angermann have tracked down Olfers's original type specimens. They have confirmed the species assignments of the type specimens and have reviewed the historical changes in nomenclature.

Unfortunately for science, the young Olfers attracted the attention of Frederick William IV of Prussia, who enlisted him as an advisor and confidant. Olfers found himself involved in a variety of projects in Berlin, notably the planning and design of the Neues Museum on the Museuminsel. He never returned to science.

The next major additions to porcupine biology came from France, in the person of Frederic Cuvier (1773–1838), the great porcupine classifier of the Napoleonic era. Frederic Cuvier worked at the National Museum of Natural History in Paris. The city was also the home of his older brother Georges, who is recognized as one of the science luminaries of his age. Georges Cuvier is remembered as the father of comparative anatomy and of paleontology.

Less interested in biological theory than his older brother, Frederic concentrated on the Linnaean task of exploring the world by describing its animals. In his position at the National Museum of Natural History in Paris, he saw a steady stream of specimens arriving from across the world. Besides the three new porcupine species, Cuvier described a long string of other mammals: otters, bats, ground squirrels, bears, armadillos, primates, even fish species. No systematist working today would claim expertise in such a broad range of taxa. The three porcupines established by Cuvier, all in 1823, were *Hystrix javanica* (Sunda porcupine), *Coendou spinosus* (Paraguay dwarf porcupine), and *Sphiggurus villosus* (orange-spined dwarf porcupine, currently included in *C. spinosus*). Cuvier's careful species descriptions are a tribute to French science of his time, which engaged the finest minds of the age in a great common effort to describe the living world.

The fourth naturalist to add to the pantheon of porcupinology was Oldfield Thomas (1858–1929), who described three new species: *Coendou vestitus* (brown dwarf porcupine), *C. pruinosus* (frosted dwarf porcupine), and *C. quichua* (Rothschild's porcupine). Thomas had been born in England but spent part of his childhood in Cape Town, South Africa, where he developed a love of natural history, collecting insects on Table Mountain. He returned to England for schooling, and in 1876, at age 18, found himself a position at the British Museum in London while continuing biological studies at the Royal College of Science. The British Museum at the time held the world's largest animal collection, with many specimens still undescribed by science. Among the famous contributors to the museum were J. J. Audubon, Charles Darwin, A. R. Wallace, and Captain James Cook.

Thomas showed enormous talent and energy in his museum work and was promoted by Dr. Gunther, the museum's keeper of zoology. Thomas's effort was prodigious. Over his lifetime, he described some 2,000 new species and subspecies of mammals, defined over 200 genera, and wrote over 1,100 books, catalogues, and scientific notes.

Thomas was well acquainted with the principle of biological variation and used it to delineate subspecies. But typically, his species descriptions were not statistically driven; rather, they were based on contrast and comparison with related forms. Thus, in describing Rothschild's porcupine, he notes it is short-haired as compared with the long-haired *Coendou mexicanus* found immediately to the north. Some spines of the back are white-tipped, and the premolars are scarcely or not at all larger than the molars. The method seems almost too easy, but it works. The porcupine species established by Thomas have not been eliminated by later research.

How do these techniques compare with the work of systematists today? In 2001, Robert Voss and Maria da Silva established two new porcupine species, *Coendou ichillus* (streaked dwarf porcupine) and *C. roosmalenorum* (Roosmalen's dwarf porcupine). Voss and da Silva point out that these two species are related to two species established previously by Thomas: *C. vestitus* and *C. pruinosus*. All four species are small (only 1.3 pounds, or 0.6 kg, for the smallest, *C. roosmalenorum*, though the animal may have been emaciated). And the pelage of all four species contains, in addition to soft fur and quills, long, flexible, barbless quills called bristle quills. Voss and da Silva then make cross species comparisons of 11 characters. They set up a matrix that differentiates the four species, shown in abbreviated form in the table.

Because no two species in the matrix show the same condition in all character states, the four can be distinguished as separate species. In their long and careful paper, Voss and da Silva also provide information about the collection sites of their specimens (hence their species ranges), about

Morphological differences between four New World porcupine species

Taxon	Belly cover	Dorsal fur	Tail	Palate keel[a]	Bullae[b]
C. vestitus	Thick fur and guard hairs	Blackish, dense	Short	Present	Small
C. pruinosus	Thick fur and guard hairs	Frosted, dense	Short	Absent	Small
C. ichillus	Sparse fur and spinous hairs	Blackish, sparse	Long	Absent	Large
C. roosmalenorum	Sparse fur and guard hairs	Gray/brown, dense	Long	Absent	Large

Source: Based on Voss and da Silva 2001.

[a] A bony ridge running down the middle of the palate.

[b] Hemispherical protrusions in the back of the skull, level with the ears. They house portions of the middle and inner ear.

available natural history and the species' conservation status, details of skull measurements, photos of living animals and skulls, speculation about ecological relationships, and literature references. The result is a detailed, multidimensional portrait of each species, not just a name and generic relationship.

In 2011, Leite and coworkers used a different approach to species taxonomy. They sequenced the cytochrome *b* genes from two specimens of the Brazilian porcupine (*Coendou prehensilis*), one from eastern and the other from western Brazil. The two specimens showed a 4.9% difference in gene sequence, probably sufficient to establish them as separate species.

The principle of establishing species on the basis of DNA sequence differences is fundamentally no different from the method used by Voss and da Silva, Oldfield Thomas, and all systematists going back to Linnaeus: a comparison of shared characters. Characteristics like quill morphology, tail length, and size of auditory bullae (bony protrusions on the back and sides of the skull adjacent to the ears) are in principle no different from the base sequences of A, T, G, and C in genes. But instead of analyzing a dozen or a couple of dozen character differences, gene sequencing allows analysis of literally thousands of codon differences. The power of gene sequencing lies in this multiplicity of comparisons.

The two specimens of *C. prehensilis* analyzed by Leite's group were similar morphologically and could be distinguished only by molecular methods. At some future time, when the species are named and officially recognized and their natural histories are studied, more sophisticated morphological analysis will be sure to reveal differences not apparent to the morphologist's eye today. Increasingly, the systematists of the future will depend on molecular methods. These methods have the power not only to differentiate individual species, but also to show evolutionary relationships between disparate forms.

How can a researcher safely mark a porcupine for identification in the wild?

The method that a researcher uses to mark porcupines depends on how he or she plans to follow the animal afterwards. All marking methods require a brief immobilization or anesthesia. A struggling porcupine can be dangerous.

A low-tech marking method involves attaching a simple collar around the neck, without a radio transmitter. Because North American porcupines have large home ranges, it might seem that a porcupine marked by collar alone would be hard to relocate in the wild, but they also sit in favorite resting trees and feeding trees in which they can be found time after time. With the use of collars of different colors, a number of animals can be distinguished in the wild. A suitable collar material is ½ to ¾-inch-wide nylon webbing, available in sporting goods stores. Collars are not placed on young, growing animals because their necks will expand. Even on adult porcupines the collars are attached loosely to allow for seasonal weight gain. And collars deployed in temperate habitats should have no metal parts touching the animal's skin; otherwise, frostbite can occur.

Tattooing is a permanent marking method that is painless to the animal and offers no impediment to movement. The tattoo is applied in the groin area, where it can be seen through the short fur. The number of animals that can be individually marked is unlimited. Of course, a tattoo requires recapture for reading.

A marking method used by many mammalogists is ear tagging. Unfortunately, the North American porcupine is a poor candidate for ear tagging. Tags are easily lost as the animal pushes through the tight confines of a tree canopy. Its ear lobes are tiny and offer little surface for anchoring the tags. In my experience, an ear tag will stay on a porcupine less than a year.

Another simple marking is with subcutaneous transponder chips. These are about the size of a grain of rice and are inserted under the skin hypodermically. Once inserted, they require no further maintenance and cause no discomfort to the animal. Unlike a radio transmitter, which can be detected from several miles away, the transponder chip returns a signal only when the detector is a few inches away. In practical terms, this means that the porcupine must be recaptured for identification. Each transponder chip is programmed with a unique ID number.

Radio collaring is the method of choice for following the movements of a porcupine in the wild. A radio collar is a small radio transmitter hung on a collar around the animal's neck. The transmitter functions like a radio station, broadcasting at a fixed frequency. To hear the signal, one listens on a tunable receiver. The signal is loudest when a directional antenna points towards the transmitter. The antenna can therefore lead one to a porcupine

up to several miles away, even if the animal is in a shallow den or inside a thick tree. Radio collars are especially well suited to New World porcupines because the animals do not run when approached. A radio collared deer will run before you see it. Again, all the strictures about expanding body size and metal-skin contact apply.

Ordinary radio collars cost several hundred dollars apiece; the receivers are even more expensive. The batteries in most cases must be replaced by the manufacturer. The typical battery life is 2 to 3 years, which means the animal must be recaptured and supplied with a fresh radio collar at regular intervals. If recapture is difficult, collars may be equipped with a detachment system that separates the collar from the animal after a predetermined time.

Advanced radio collars can be linked to global positioning systems (GPS), which provide round-the-clock information on an animal's movements. The information is collected in a memory chip in the radio collar and downloaded remotely or when the animal is recaptured or when the collar is time-released. Such data can give information on an animal's home range, social interactions, births and maternal care, dispersal, activity cycles, and much more. With a current price tag of several thousand dollars per collar, this revolutionary technology requires a significant financial commitment.

What don't we know about porcupines?

Given that the first scientific study of the North American porcupine was published in 1727, we are approaching the end of the third century of study for this animal. One might ask whether anything is left to discover, but the large body of study has only increased the range of unknowns surrounding this and other porcupines. The study of an animal is like the study of a great forest: not until one enters the forest does one become aware of its size, diversity, and unique features. I offer here some topics in porcupine biology that remain unknown today, with the guarantee that answers to these questions will raise an endless number of others.

- What are the evolutionary relationships of the New World and Old World porcupines, and the relationships within the two groups, particularly those of the New World? How many species are there? Are all the morphological species valid? Are there still-undescribed crypto-species?
- What ecosystem effects do porcupines have? Diner and coworkers have shown that the North American porcupine has the potential for forcing evolutionary change in some of its food species. How do porcupine-filled forests differ from similar forests from which the porcupines are absent?

- How are the New World porcupines separated in terms of feeding choice, habitat preferences, antipredator strategies, and so on? We know nothing about the behavior in the wild of most South American species. The few species that have been studied, have not been studied in depth.
- The North American porcupine shows female-biased juvenile dispersal. Is the same true in other porcupine species? Dispersal patterns have a strong influence on social structure, but no one has investigated the dispersal patterns in the other porcupines.
- We do not have a DNA fingerprint analysis of the population of any porcupine species. Such data would indicate both the variance of reproductive success and sexual biases in patterns of dispersal. The required molecular genetics has not been done.
- Why does the species range of the North American porcupine leave the southeastern United States unoccupied? While the porcupine is found in such southern regions as parts of Texas and New Mexico, it is absent in Louisiana, Mississippi, Alabama, Florida, and the other southeastern states. These states have abundant forest cover, and fossil evidence shows that porcupines lived there in the past. Is an unrecognized parasite present in the area? Are suitable food trees absent? What would happen to a dozen Maine porcupines released in, say, Alabama?
- Both New World and Old World porcupines carry intestinal nematodes of the genus *Wellcomia*. The evolutionary relationships of the nematodes parallel the evolutionary relationships of the porcupines, suggesting that the nematode symbionts have been highly conserved. This raises the possibility that the nematodes may in fact be mutualists, benefiting their hosts, instead of parasites. What physiological role do the nematodes play in their hosts?
- The North American porcupine carries quill antibiotics. I have suggested that the antibiotics limit damage from self-quilling, a recurrent event in an arboreal lifestyle. Do other New World porcupine species carry quill antibiotics, and if so, what are they? It appears unlikely that quill antibiotics will be found in most *Coendou* species, since they don't fall out of trees. But the situation may be different with *C. rufescens*, whose tail is proportionately the shortest in the *Coendou* group.
- The North American porcupine disseminates a warning odor when confronting a predator. Do other porcupines do the same? The observation of Voss and Emmons that South American porcupine dens have a strong odor suggests that a warning odor may be present. If so, do different species use the same warning odor? Are there any Batesian mimics that lack the porcupine's defense capability but cheat its predators by mimicking the porcupine's warning odor?

- All porcupines have an unusual penile structure called the sacculus urethralis. The sacculus is an invagination in the tip of the penis that is everted during copulation and deploys large spines against the vaginal wall. What is the role of the spines? Do they induce orgasm or ovulation in the female?
- North American porcupines, as well as a range of other Hystricomorph rodents, engage in urine showering as part of courtship and other behaviors. What is the physiological basis of the male's showering of the female with urine? Does it accelerate ovulation in the female, as has been shown in mice? None of the experiments have been performed in porcupines.
- The urine of the North American porcupine contains a small but constant level of the plasma protein albumin. Since protein is a limiting nutrient for the porcupine, its loss in the urine carries a significant nutritional cost. What benefits accrue to the porcupine to offset this cost?
- All porcupines have perineal glands—paired invaginated structures between the urethra and the anus. What role do the glands play? In Old World Cape porcupines, the glands are used to scent-mark food sources and territorial boundaries. In male North American porcupines, activation of the glands requires elevated testosterone levels. What activates the glands in the females, and how are they used?
- In North American porcupines, males can mate with multiple females. But successful mating requires the achievement of dominant status, a process typically requiring about four years. How complete is the dominance: does the dominant male copulate with all females in his territory? How long does the dominant status last? If a dominant loses his position, can the usurper be one of his own sons?
- At least one female North American porcupine lived long enough in the wild to go through menopause. Can this be demonstrated in other females? Does it happen in other porcupine species? What roles do the menopausal females (and post-dominant males) play in their populations?
- Do populations of the North American porcupine undergo long-term population cycles? Two studies based on dendrochronology (count of tree growth rings) suggest such cycles, but neither verified the cycling by measuring population densities directly. If cycling does occur, is it driven by changes in food supply or by predator pressure?
- A study of North American porcupines in the Catskill Mountains region shows that the animals engage in clay feeding. Does this occur in other parts of the animal's species range, including regions which are not sodium-depleted? And does clay feeding occur in other porcupine species?

- North American porcupines have an unerring ability to detect sodium, an essential nutrient for all animals. Since sodium salts have no odor, what cues do the animals use to find it?
- Humans living in iodine-depleted regions such as mountainous or deep-inland areas require supplements of dietary iodine to avoid development of goiters, cretinism, and other effects of iodine insufficiency. Do porcupine populations from iodine-poor areas suffer from similar iodine insufficiencies? If not, what do the animals use as iodine sources?
- North American porcupines follow individually specialized diets—that is, the feeding choices of individuals are narrower than the feeding choices of the population as a whole. It has been suggested that this reflects specializations of individual gut microflora. Can this be confirmed experimentally? And do other New World porcupines show similar feeding specializations?
- North American porcupines have an internal sodium pool in their caecal fluid. Is this also true of other porcupine species? Is there a New versus Old World difference in this respect? (The two groups have different diets.)
- What is the function of the barbulated quills (illustrated on page 43) of the brush-tailed porcupines (*Atherurus* spp)? Since the barbules can be expected to compromise the piercing function of the quills, what alternate function do they serve?
- Scabies is a comparatively recent disease of North American porcupines, having been first reported only in 1958 by Payne and O'Meara. This suggests that the porcupine acquired its scabies mite from some other host species. What was the host species, and what were the circumstances of transmission?
- The North American porcupine does not require a supply of drinking water in the wild. One mechanism for reducing water demand in other animals is the recycling of urea by the intestinal bacteria. Urea recycling also reduces dietary nitrogen demand. Is this mechanism present in porcupines?
- What are the foraging patterns of *Erethizon* in the heart of its species range, the boreal forest of Canada? Most studies have been carried out in mixed deciduous forests, mountain forests, or other peripheral areas whose forest structure is very different.

We can list more unknowns about porcupines than there are letters in the alphabet. This is fortunate, because it makes us focus more carefully on the animals before us. But mysteries arise by the process of deeper engagement. As we learn more about these unique animals in the broad march of biology, new and untrodden paths branch out that lead to mysteries still undreamed of.

Appendix A

Porcupines of the World

Order Rodentia

Scientific Name	Common Name	General Location
Family Hystricidae		
Hystrix africaeaustralis	Cape porcupine	S Africa to Tanzania and Congo River
Hystrix cristata	Crested porcupine	N Africa and Italy
Hystrix indica	Indian crested porcupine	Turkey, Syria, Israel east to S Kazakhstan, India, Sri Lanka
Hystrix brachyura	Himalayan, or Malayan, porcupine	India to S China, south to Malaysia, Sumatra, Borneo
Hystrix crassispinis	Thick-spined porcupine	Borneo
Hystrix javanica	Sunda porcupine	Java, Bali
Hystrix pumila	Philippines porcupine (v)	Philippines
Hystrix sumatrae	Sumatran porcupine	Sumatra
Atherurus africanus	African brush-tailed porcupine	Gambia, Ghana, to Sudan, Kenya
Atherurus macrourus	Asiatic brush-tailed porcupine	NE India to S China, south to Malay Peninsula
Trichys fasciculata	Long-tailed porcupine	Sumatra, Borneo, SW Malay Peninsula
Family Erethizontidae		
Subfamily Erethizontinae		
Coendou bicolor	Bicolored-spined porcupine	Andean foothills of Colombia south to Peru, Bolivia
Coendou ichillus	Streaked dwarf porcupine (dd)	E Ecuador, NE Peru
Coendou insidiosus	Bahia dwarf porcupine	SE Brazil
Coendou melanurus	Black-tailed porcupine	East of Negro, north of Amazon to Venezuela, Guianas, N Brazil
Coendou mexicanus	Mexican hairy porcupine	S Mexico to Panama
Coendou nycthemera	Black dwarf porcupine	South of lower Amazon

Coendou prehensilis	Brazilian porcupine	South America east of Andes, south to NW Argentina, E Paraguay
Coendou pruinosus	Frosted dwarf porcupine	E Colombia, W Venezuela
Coendou quichua	Rothschild's porcupine	Panama to NW Colombia
Coendou roosmalenorum	Roosmalen's dwarf porcupine (dd)	Brazil – Madeira River
Coendou rufescens	Stump-tailed porcupine	Mountains of Colombia, Ecuador, N Peru; disjunct in N Bolivia
Coendou spinosus	Paraguay dwarf porcupine	SE Brazil to E Paraguay, NE Argentina, N Uruguay
Coendou vestitus	Brown dwarf porcupine (dd)	E Colombia
Erethizon dorsatum	North American porcupine	Alaska, Canada, W and NE USA
Subfamily Chaetomyinae		
Chaetomys subspinosus	Thin-spined porcupine (v)	SE Brazil

dd – data deficient v – vulnerable

Appendix B

Worldwide Wildlife Rehabilitation Organizations

Brazil

Brazilian Institute of Environmental and Renewable Natural Resources (IBAMA)
www.ibama.gov.br/fauna-silvestre
Juciara Elise Pelles, coordinator of IBAMA fauna department
fauna.sede@ibama.gov.br
SOS Fauna (in process of establishment)
http://sosfauna.braslink.com/e_reintr.htm

Canada

Alberta Wildlife Rehabilitators Association
www.albertawildliferehab.org
Wildlife Rescue Association of British Columbia
www.wildliferescue.ca/team.shtml
Alberta, Saskatchewan, and Manitoba rehabilitator links
www. ec.gc.ca/nature

Chile

Wildlife Rescue and Rehabilitation Centers for Forest Fauna, Chile
www.surmagico.cl/centros_rehabilitacion_chile.htm

China

Southeast Guandong Avian Care
greenheron@asia.com *or* kimberly4birds@asia.com

Costa Rica

Jardin Gaia Wildlife Rescue Center (parrots, primates)
wildlife@cariari.ucr.ac.cr

Great Britain

British Wildlife Rehabilitation Council
www.bwrc.org.uk

India

Bangalore, Karnataka Animal Welfare Organization (snakes, other)
zarirb@vsnl.com

Indonesia

Jakarta, Tegal Alur Wildlife Rescue Center
ptsta@telkom.net

Israel

Israeli Wildlife Hospital and Rehabilitation Center
www.latevanolad.org.il/english/
Society for the Protection of Nature in Israel (Carmel, Northern Region)
Telephone: 057 727620

Italy

Florence: Dr. S. Scoccianti, Centro Recupero Annimali Selvatici
Telephone: 0338-2839540
Milan: Ente Nazionale Protezione Animali
enpami@iol.it

Mexico

Santiago de Queretaro (falcons): Enrique Valverde
Telephone : (42) 340330 171812

South Africa

Cape Province: African Dawn Bird and Animal Sanctuary
aztecg@exite.co.uk
Western Cape: Monkeyland Primate Sanctuary (primates, mammals, birds):
monkeys@global.co.za
Northern Region: FreeMe Wildlife Rehabilitation Centre
freeme@iburst.co.za

United States

National Wildlife Rehabilitators Association
www.nwrawildlife.org

Links to U.S. wildlife rehabilitators in individual states
www.wildliferehabilitators.com/links.htm

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Bibliography

Ahnelt, P. K., and H. Kolb. 2000. The mammalian photoreceptor mosaic-adaptive design. *Progress in Retinal and Eye Research* 19(6):711–77.

Ahnelt, P., K. Moutairou, M. Glossmann, and A. Kubber-Heiss. 2003. Lack of S-opsin expression in the brush-tailed porcupine (*Atherurus africanus*) and other mammals: Is the evolutionary persistence of S-cones a paradox? Pages 31–38 in: J. D. Mollon, J. Pokorny, and K. Knoblauch, eds., *Normal and Defective Color Vision*. Oxford University Press, New York.

Alexander, A. J. 1956. Bone carrying by a porcupine. *South African Journal of Science* 52:257–58.

Alkon, P. U. 1999. Microhabitat to landscape impacts: Crested porcupine digs in the Negev Desert highlands. *Journal of Arid Environments* 41:183–202.

Alkon, P. U., and D. Salz. 1988a. Foraging time and northern range limits of Indian crested porcupine (*Hystrix indica* Kerr). *Journal of Biogeography* 15:403–8.

Alkon, P. U., and D. Saltz. 1988b. Influence of season and moonlight on temporal activity patterns of Indian crested porcupines (*Hystrix indica*). *Journal of Mammalogy* 69(1):71–80.

Barnes, J. 1993. *The Porcupine*. Vintage Books, New York.

Barthelmess, E. 2006. *Hystrix africaeaustralis. Mammalian Species* 788(1):1–7.

Bartos, C. Husbandry standards for keeping porcupines in captivity. Peoria (Ill.) Zoo Website. www.glenoakzoo.org/RodentTAG/rodentPDFs/PorcupineStandards.pdf.

Baryshnikov, G. F. 2003. Pleistocene small porcupine from the Ural Mountains, Russia, with note on taxonomy of *Hystrix vinogradovi* (Rodentia, Hystricidae). *Russian Journal of Theriology* 2:43–47.

Beck, B. E. F., P. J. Claus, P. Goswami, and J. Handoo, eds. 1999. *Folktales of India*. University of Chicago Press, Chicago.

Belloc, H. 1951. *The Verse of Hillaire Belloc*. Ed. W. N. Roughead. J. B. Lippincot, Philadelphia.

Bergstrom, D., A. Kiefer, A. Lucieer, J. Wasley, L. Pedersen, and S. Chown. 2009. Indirect effects of invasive species removal devastate World Heritage island. *Journal of Applied Ecology* 46:73–81.

Berteaux, D., I. Klvana, and C. Trudeau. 2005. Spring-to-fall mass gain in a northern population of North American porcupines. *Journal of Mammalogy* 86(3):514–19.

Blund, T. 2003. Genghis Khan: Most prolific man in history? *Science*, Feb. 9, 2003.

Bonvicino, C. R., V. Penna-Firme, and E. Braggio. 2002. Molecular and karyotypic evidence of the taxonomic status of *Coendou* and *Sphiggurus* (Rodentia: Hystricognatha). *Journal of Mammalogy* 83(4):1071–76.

Bounds, D. L., M. H. Sherfy, and T. A. Mollett. 2003. Nutria. Pages 1119–47 in: G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds., *Wild Mammals of North America*. 2nd ed. Johns Hopkins University Press, Baltimore.

Bradley, S. R., and D. R. Deavers. 1980. A re-examination of the relationship between thermal conductance and body weight in mammals. *Comparative Biochemistry and Physiology A* 65:465–76.

Bragg, C. J., J. D. Donaldson, and P. G. Ryan. 2004. Density of Cape porcupines in a semi-arid environment and their impact on soil turnover and related ecosystem processes. *Journal of Arid Environments* 61(2):261–75.

Brain, C. K. 1980. Some criteria for the recognition of bone-collecting agencies in African caves. Pages 107–30 in: A. K. Behrensmeyer and A. P. Hill, eds., *Fossils in the Making: Vertebrate Taphonomy and Paleoecology*. University of Chicago Press, Chicago.

Brightsmith, D. J., and R. A. Munoz-Najar. 2004. Avian geophagy and soil characteristics in southeast Peru. *Biotropica* 36:534–43.

Brodie, E. D., Jr. 1977. Hedgehogs use toad venom in their own defense. *Nature* 268:627–28.

Brown, Thomas. 1720. *The remains of Mr. Tho. Brown, serious and comical, in prose and verse*. Facsimile edition, 2010. Gale ECCO Print Editions.

Campbell, K. L., and R. A. MacArthur. 1997. Urea recycling in muskrats (*Ondatra zibethicus*): A potential nitrogen conservation tactic? *Physiological Zoology* 70(2):222–29.

Chapman, D. M., and U. Roze. 1997. Functional histology of quill erection in the porcupine (*Erethizon dorsatum*). *Canadian Journal of Zoology* 75:1–10.

Charles-Dominique, P., M. Atramentowicz, M. Charles-Dominique, H. Gerard, A. Hladik, and M. F. Prevost. 1981. Les mammiferes frugivores arboricoles nocturnes d'une foret Guyanaise: Inter-relations plantes-animaux. *Annual Review of Ecology* 35:341–435.

Clutton-Brock, T. H. 1988. *Reproductive Success*. University of Chicago Press, Chicago.

Coltrane, J. A., and P. S. Barboza. 2010. Winter as a nutritional bottleneck for North American Porcupines (*Erethizon dorsatum*). *Journal of Comparative Physiology B* 180:905–18.

Coltrane, J. A., S. Farley, P. S. Barboza, F. Kohl, R. Sinnott, and B. M. Barnes. 2011. Seasonal body composition, water turnover, and field metabolic rates in porcupines (*Erethizon dorsatum*) in Alaska. *Journal of Mammalogy* 92(3):601–10.

Corbet, G. B., and L. A. Jones. 1965. The specific characters of the crested porcupines, subgenus *Hystrix*. *Journal of Zoology* (London) 144:285–300.

Corbet, N. U., and R. J. Van Aarde. 1996. Social organization and space use in the Cape porcupine in a southern African savanna. *African Journal of Ecology* 34:1–14.

Cott, P. A., and N. J. Mochnacz. 2007. Bull trout, *Salvelinus confluentus*, and North American porcupine, *Erethizon dorsatum*, interaction in the Mackenzie Mountains, Northwest Territories. *Canadian Field-Naturalist* 121(4):438–39.

Cottam, C., and C. S. Williams. 1943. Speed of some wild mammals. *Journal of Mammalogy* 24:262–63.

Courlander, H., and E. Arno 1959. *The Tiger's Whisker, and Other Tales and Legends from Asia and the Pacific*. Harcourt, Brace, New York.

Craig, E. H., and B. L. Keller. 1986. Movements and home range of porcupines, *Erethizon dorsatum*, in Idaho shrub desert. *Canadian Field-Naturalist* 100:167–73.

DeMatteo, K. E., and H. J. Harlow. 1997. Thermoregulatory responses of the North American porcupine (*Erethizon dorsatum bruneri*) to decreasing ambient temperature and increasing wind speed. *Comparative Biochemistry and Physiology B* 116:339–346.

de Souto Lima, R. B. S., P. A. Oliveira, and A. G. Chiarello. 2009. Diet of the thin-spined porcupine (*Chaetomys subspinosus*), an Atlantic forest endemic threatened with extinction in southeastern Brazil. *Mammalian Biology* 75:538–46.

de Villiers, M. S., R. J. Van Aarde, and H. M. Dott. 1994. Habitat utilization by Cape porcupines (*Hystrix africaeaustralis*) in a savanna ecosystem. *Journal of Zoology* 232(4):539–49.

Diner, B., D. Berteaux, J. Fyles, and R. L. Lindroth. 2009. Behavioral archives link the chemistry and clonal structure of trembling aspen to the food choice of the North American porcupine. *Oecologia* 160:687–95.

Dodge, W. E., 1967. The biology and life history of the porcupine (*Erethizon dorsatum*) in western Massachusetts. Ph.D. diss. University of Massachusetts, Amherst.

Doutt, J. K., C. A. Heppenstall, and J. E. Guilday. 1977. *Mammals of Pennsylvania*. 4th ed. Pennsylvania Game Commission, Harrisburg.

Durrell, G. 1954. *The Bafut Beagles*. Tower Publications, New York.

Earle, R. D., and K. R. Kramm. 1980. Techniques for age determination in the Canadian porcupine. *Journal of Wildlife Management* 44(2):413–19.

Emmons, L. H. 1983. A field study of the African brush-tailed porcupine, *Atherurus africanus*, by radiotelemetry. *Mammalia* 47:183–94.

Emmons, L. H. 1997. *Neotropical Mammals: A Field Guide*. 2nd ed. University of Chicago Press, Chicago.

Erdrich, L. 2008. *The Porcupine Year*. Harper Collins, New York.

Estrada, A., and R. Coates-Estrada. 1985. A preliminary study of resource overlap between howling monkeys (*Alouatta palliata*) and other arboreal mammals in the tropical rain forest of Los Tuxtlas, Mexico. *American Journal of Primatology* 9:27–37.

Felicetti, L. A., L. A. Shipley, G. W. Witmer, and C. T. Robbins. 2000. Digestibility, nitrogen excretion, and mean retention time by North American porcupines (*Erethizon dorsatum*). *Physiological and Biochemical Zoology* 73(6):772–80.

Freeman, R. S. 1949. Notes on the morphology and life cycle of the genus *Monoecocestus* Beddard, 1914 (Cestoda: Anoplocephalidae), from the porcupine. *Journal of Parasitology* 35:605–12.

Garland, T. 1983. The relation between maximum running speed and body mass in terrestrial mammals. *Journal of Zoology* (London) 199:157–70.

Gilardi, J. D., S. S. Duffey, C. A. Munn, and L. A. Tell. 1999. Biochemical functions of geophagy in parrots: Detoxification of dietary toxins and cytoprotective effects. *Journal of Chemical Ecology* 25:897–922.

Gine, G. A. F., J. M. B. Duarte, and D. Faria. 2010. Feeding ecology of a selective folivore, the thin-spined porcupine (*Chaetomys subspinosus*) in the Atlantic Forest. *Journal of Mammalogy* 91(4):931–41.

Good, Peter, J. A. Lowe, M. Collins, and W. Moufouma-Okia. 2008. An objective tropical Atlantic sea surface temperature gradient index for studies of south Amazon dry-season climate variability and change. *Philosophical Transactions of the Royal Society of London B* 363(1498):1761–66.

Gosling, L. M. 1980. Reproduction of the Himalayan porcupine (*Hystrix hodgsoni*) in captivity. *Journal of Zoology* (London) 192:546–49.

Grand, T. I., and J. F. Eisenberg. 1982. On the affinities of the Dinomyidae. *Saugetierkundliche Mitteilungen* 30:151–57.

Griesemer, S. J., T. K. Fuller, and R. M. DeGraaf. 1996. Denning patterns of porcupines, *Erethizon dorsatum*. *Canadian Field-Naturalist* 110(4):634–37.

Haim, A. R., R. J. Van Aarde, and J. D. Skinner. 1992. Urinary characteristics of the Cape porcupine, *Hystrix africaeaustralis*: Effects of photoperiod and temperature. *Journal of Basic and Clinical Physiology and Pharmacology* 3:165–75.

Hale, M. B., and T. K. Fuller. 1996. Porcupine (*Erethizon dorsatum*) demography in central Massachusetts. *Canadian Journal of Zoology* 74: 480–84.
Handley, C. O., and R. H. Pine. 1992. A new species of prehensile-tailed porcupine, genus *Coendou* Lacepede, from Brazil. *Mammalia* 56:237–44.
Hardin, G. 1959. *Nature and Man's Fate*. Mentor, New York.
Hogan, L. 1996. *Dwellings: A Spiritual History of the Living World*. Simon and Schuster, New York.
Holdo, R. M., J. P. Dudley, and L. R. McDowell. 2002. Geophagy in the African elephant in relation to availability of dietary sodium. *Journal of Mammalogy* 83: 632–64.
Huchon, D., F. Catzeflis, and E. J. P. Douzery. 2000. Variance of molecular datings, evolution of rodents, and the phylogenetic affinities between Ctenodactylidae and Hystricognathi. *Proceedings of the Royal Society of London B* 267:393–402.
Huchon, D., and E. J. P. Douzery. 2001. From the Old World to the New World: A molecular chronicle of the phylogeny and biogeography of Hystricognath rodents. *Molecular Phylogenetics and Evolution* 20(2):238–51.
D. Huchon, O. Madsen, M. J. J. B. Sibbald, K. Ament, M. J. Stanhope, F. Catzeflis, W. W. deJong, and E. J. P. Douzery. 2002. Rodent phylogeny and a timescale for the evolution of Glires: Evidence from an extensive taxon sampling using 3 nuclear genes. *Molecular Biology and Evolution* 19:1053–65.
Hugot, J.-P. 2002. New evidence of Hystricognath rodent monophyly from the phylogeny of their pinworms. *Bulletin du Museum d'Histoire Naturelle* (Paris) 8:133–38.
Jango-Cohen, J. 2005. *Porcupines*. Marshall Cavendish Benchmark, New York.
Johnson, M. D., K. D. Magnusson, C. L. Shmon, and C. Waldner. 2006. Porcupine quill injuries in dogs: A retrospective of 296 cases, 1998–2002. *Canadian Veterinary Journal* 47(7):677–82.
Jones, M. L. 1982. Longevity of captive mammals. *Der Zoologische Garten* 52:113–28.
Jori, F., M. Lopez-Bejar, and P. Houben. 1998. The biology and use of the African brush-tailed porcupine (*Atherurus africanus*, Gray, 1842) as a food animal: A review. *Biodiversity and Conservation* 7(11):1417–26.
Kalmbach, E. R. 1953. Trout encounters porcupine. *Journal of Mammalogy* 34(4):511.
Kaula, E. M. 1968. *African Village Folktales*. World Publishing, Cleveland.
Kay, E. H., and H. E. Hoekstra. 2008. Rodents. *Current Biology* 18:R406–10.
Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patterson. 2007. Oliver P. Pearson: Scientist, statesman, gentleman. Pages 1–16 in: D. A. Kelt, E. P. Lessa, J. Salazar-Bravo, and J. L. Patterson, eds., *The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson*. University of California Press, Berkeley and Los Angeles.
Khan, A. A., S. Ahmad, I. Hussain, and S. Munir. 2000. Deteriorating impact of Indian crested porcupine, *Hystrix indica*, on forestry and agricultural systems in Pakistan. *International Biodeterioration and Biodegradation* 45:143–49.
Kinnell, G. 2000. *A New Selected Poems*. Houghton Mifflin, Boston.
Kitamura, S., S. Thong-Aree, S. Madsri, and P. Poonswad 2010. Mammal diversity and conservation in a small isolated forest of southern Thailand. *Raffles Bulletin of Zoology* 58(1):145–56.
Klvana, I., D. Berteaux, and B. Cazelles. 2004. Porcupine feeding scars and climatic data show ecosystem effects of the solar cycle. *American Naturalist* 164: 283–97.
Kurten, B., and E. Anderson. 1980. *Pleistocene Mammals of North America*. Columbia University Press, New York.

Landry, S. O. 1957. *The Interrelationships of the New and Old World Hystricomorph Rodents*. University of California Publications in Zoology, vol. 56, no. 1. University of California Press: Berkeley.

Lang, A., and W. Lynch. 2006. *Baby Porcupine*. Fitzhenry and Whiteside, Markham, Ontario.

Lawton, J. H., and C. G. Jones. 1995. Linking species and ecosystems: Organisms as ecosystem engineers. Pages 141–50 in: C. G. Jones and J. H. Lawton, eds., *Linking Species and Ecosystems*. Chapman and Hall, New York.

Leite, Y. L. R., V. Caldara Jr., A. C. Loss, L. P. Costa, E. R. A. Melo, J. R. Gadella, and A. R. M. Pontes 2011. Designation of a neotype for the Brazilian porcupine, *Coendou prehensilis* (L. 1758). *Zootaxa* 2791:30–40.

Levi-Strauss, C. 2000. The environment of myth. Pages 132–34 in: L. Coupe, ed., *The Green Studies Reader: Romanticism to Ecocentrism*. Routledge Press, London.

Li, G., U. Roze, and D. Locke 2007. Warning odor of the North American porcupine (*Erethizon dorsatum*). *Journal of Chemical Ecology* 23: 2737–54.

Luckett, W. P., and J.-L. Hartenberger, eds. 1985. *Evolutionary Relationships among the Rodents*. Plenum Press, New York.

Luepnitz D. A. 2003. *Schopenhauer's Porcupines: Intimacy and Its Dilemmas*. Basic Books, New York.

Mabille, G., S. Descamps, and D. Berteaux 2010. Predation as a possible mechanism relating winter weather to population dynamics in a North American porcupine population. *Population Ecology* 52:537–46.

Macdonald, D. W., K. Kranz, and R. T. Aplin. 1984. Behavioral, anatomical, and chemical aspects of scent marking amongst capybaras, *Hydrochoerus hydrochaeris* (Rodentia: caviomorpha). *Journal of Zoology* (London) 202:341–60.

Markle, S. 2008. *Porcupines: Animal Prey*. Lerner Publications, Minneapolis.

Markowitz, C. 2008. Is the broken Hubble telescope worth saving? *USA Today*, Oct. 1, 2008.

Massolo, A., F. R. Dani, and N. Bella. 2009. Sexual and individual cues in the perianal gland secretum of crested porcupines (*Hystrix cristata*). *Mammalian Biology* 74(6):488–96.

McDade, H. C., and W. B. Crandall. 1958. Perforation of the gastrointestinal tract by an unusual foreign body—a porcupine quill. *New England Journal of Medicine* 258:746–47.

McDowell, W. S. 2001. Porcupine lessons. *Harvard University Gazette*, June 7, 2001.

McGovern, A. 1990. *Aesop's Fables*. Scholastic, New York.

McLean, R. G., A. B. Carey, L. J. Kirk, and D. B. Francy. 1993. Ecology of porcupines (*Erethizon dorsatum*) and Colorado tick fever virus in Rocky Mountain National Park, 1975–1977. *Journal of Medical Entomology* 30(1):236–38.

Medway, W., D. L. Skand, and C. F. Sarver. 1989. Neurological signs in American porcupines (*Erethizon dorsatum*) infected with *Baylisascaris* and *Toxoplasma*. *Journal of Zoo and Wildlife Medicine* 20(2):207–11.

Meredith, R. W., et al. 2011. Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science* 334:521–24.

Milton, K. 1980. T*he Foraging Strategy of Howler Monkeys*. Columbia University Press, New York.

Miura, S., M. Yasuda, and L. C. Ratnam. 1997. Who steals the fruits? Monitoring frugivory of mammals in a tropical rain forest. *Malayan Nature Journal* 50: 183–93.

Mohr, E. 1965. *Altweltliche Stachelschweine*. A. Ziemsen Verlag, Wittenberg Lutherstadt, Germany.
Montgomery, D. 2010. Natural history and ecology of porcupines at Buffalo Lake National Wildlife Refuge in the Texas panhandle. M.Sc. thesis, West Texas A&M University, Canyon, TX.
Muller-Schwarze, D., N. J. Volkman, and K. F. Zemanek. 1977. Osmetrichia, specialized scent hairs in black-tailed deer. *Journal of Ultrastructure Research* 59: 223–30.
Murphy, W. J., R. Stanyon, and S. J. O'Brien. 2001. Evolution of mammalian genome organization inferred from comparative gene mapping. *Genome Biology* 2(6):1–8.
Novotny, M. V. 2003. Pheromones, binding proteins, and receptor responses in rodents. *Biochemical Society Transactions* 31:117–23.
Nowak, R. M. 1999. *Walker's Mammals of the World*. 6th ed. Johns Hopkins University Press, Baltimore.
Oliveira, P. A., R. B. de Souto Lima, and A. G. Chiarello. 2012. Home range, movements, and diurnal roosts of the endangered thin-spined porcupine, *Chaetomys subspinosus* (Rodentia: Erethizontidae) in the Brazilian Atlantic forest. *Mammalian Biology* 77(2):97–107.
Passamani, M. 2009. Use of space and activity pattern of *Sphiggurus villosus* (F. Cuvier 1823) from Brazil (Rodentia: Erethizontidae). *Mammalian Biology*. doi:10.1016/j.mambio.2009.04.005.
Payne, D. D., and D. C. O'Meara. 1958. *Sarcoptes scabiei* infestation of a porcupine. *Journal of Wildlife Management* 22:321–22.
Pei, K. J.-C., Y.-C. Lai, R. T. Corlett, and K.-Y. Suen. 2010. The larger mammal fauna of Hong Kong: Species survival in a highly degraded landscape. *Zoological Studies* 49(2):253–64.
Peichl, L. 2005. Diversity of mammalian photoreceptor properties: Adaptations to habitat and lifestyle? *Anatomical Record Part A* 287A:1001–12.
Pliny the Elder. 1856. *The Natural History*. Ed. John Bostock and H. T. Riley. London.
Po-Chedley, D. S., and A. R. Shadle. 1955. Pelage of the porcupine, *Erethizon dorsatum*. *Journal of Mammalogy* 56:84–95.
Pocock, R. I., 1922. On the external characters of some Hystricomorph rodents. *Proceedings of the Zoological Society* (London) 25:365–427.
Poux, C., P. Chevret, D. Huchon, W. de Jong, and E. Douzery. 2006. Arrival and diversification of Caviomorph rodents and Platyrrhine primates in South America. *Systematic Biology* 55(2):228–44.
Powell, R. A. 1993. *The Fisher: Life History, Ecology, and Behavior*. 2nd ed. University of Minnesota Press, Minneapolis.
Roberts, M., S. Brand, and E. Maliniak. 1985. The biology of captive prehensile-tailed porcupines, *Coendou prehensilis*. *Journal of Mammalogy* 66:476–82.
Romero, Simon. 2008. A month to conjure luck with sacrifices in fire. *New York Times*, Aug. 21, 2008, A12.
Rowe, D. L., K. A. Dunn, R. M. Adkins, and R. L. Honeycutt. 2010. Molecular clocks keep dispersal hypothesis afloat: Evidence from trans-Atlantic rafting by rodents. *Journal of Biogeography* 37:305–24.
Roze, U. 1984. Winter foraging by individual porcupines. *Canadian Journal of Zoology* 62:2425–28.

Roze, U. 2006. Smart weapons. *Natural History* 115(2):48–53.
Roze, U. 2009. *The North American Porcupine*. 2nd ed. Cornell University Press, Ithaca, NY.
Roze, U., K. T. Leung, E. Nix, G. Burton, and D. M. Chapman. 2010. Microanatomy and bacterial flora of the perineal glands of the North American porcupine, *Erethizon dorsatum* (L., 1758). *Canadian Journal of Zoology* 88:59–68.
Roze, U., D. C. Locke, and N. Vatakis. 1990. Antibiotic properties of porcupine quills. *Journal of Chemical Ecology* 16:725–34.
Sackett, L. W. 1913. *The Canada Porcupine: A Study of the Learning Process*. Behavioral Monographs, vol. 2. Holt, Cambridge.
Santos, I. B., W. L. R. Oliver, and A. B. Rylands. 1987. Distribution and status of two species of tree porcupines, *Chaetomys subspinosus* and *Sphiggurus insidiosus*, in south-east Brazil. *Dodo: Journal of the Jersey Wildlife Preserve Trust* 24:43–60.
Schmidt-Nielsen, K. 1964. *Desert Animals: Physiological Problems of Heat and Water*. Dover, New York.
Schuur, E. A. G., et al. 2008. Vulnerability of permafrost carbon to climate change: Implications for the total carbon cycle. *Bioscience* 58(8):701–14.
Shadle, A. R. 1944. The play of American porcupines (*Erethizon dorsatum epixanthum*). *Journal of Comparative Physiology* 37:145–50.
Shadle, A. R., M. Smelzer, and M. Metz. 1946. The sex reactions of porcupines (*Erethizon dorsatum*) before and after copulation. *Journal of Mammalogy* 27:116–21.
Shoumatoff, A. 2007. Dispatch #40: Brazil's Mata Atlantica**:** The critically endangered coastal rainforest of Brazil, with a postscript on the musicality of birdsong. www.dispatchesfromthevanishingworld.com.
Siegenthaler, U., and J. L. Sarmiento 1993. Atmospheric carbon dioxide and the ocean. *Nature* 365:119–26.
Smith, A. T., and Y. Xie. 2008. *A Guide to the Mammals of China*. Princeton University Press, Princeton.
Sorci, G., A. Pape-Moller, and T. Boulinier. 1997. Genetics of host-parasite interactions. *Trends in Ecology and Evolution* 12(5):196–200.
Spencer, D. A. 1950. Porcupines: Rambling pincushions. *National Geographic* 98:247–64.
Spencer, D. A. 1964. Porcupine population fluctuations in past centuries revealed by dendrochronology. *Journal of Applied Ecology* 1:127–49.
Sutton, J. F. 1972. Notes on skeletal variation, tooth replacement, and cranial suture closure of the porcupine, *Erethizon dorsatum*. *Tulane Studies in Zoology and Botany* 19:56–62.
Sweitzer, R. A. 2003. Breeding movements and reproductive activities of porcupines in the Great Basin Desert. *Western North American Naturalist* 63:1–10.
Sweitzer, R. A., and J. Berger. 1992. Size-related effects of predation on habitat use and behavior of porcupines (*Erethizon dorsatum*). *Ecology* 73:867–75.
Sweitzer, R. A., and J. Berger. 1993. Seasonal dynamics of mass and body condition in Great Basin porcupines (*Erethizon dorsatum*). *Journal of Mammalogy* 74(1):198–203.
Sweitzer, R. A., and J. Berger. 1997. Sexual dimorphism and evidence for intrasexual selection from quill impalements, injuries, and mate guarding in porcupines (*Erethizon dorsatum*). *Canadian Journal of Zoology* 75:847–54.
Sweitzer, R. A., and D. W. Holcombe. 1993. Serum-progesterone levels and pregnancy rates in Great Basin porcupines (*Erethizon dorsatum*). *Journal of Mammalogy* 74(3):769–76.

Sweitzer, R. A., S. H. Jenkins, and J. Berger. 1997. Near-extinction of porcupines by mountain lions and consequences of ecosystem change in the Great Basin desert. *Conservation Biology* 11(6):1407–17.

Thomas, M. R. O. 1902. A new porcupine species, *Coendou rothschildi*. *Annals and Magazine of Natural History*, ser. 7, 10:169.

Thomas, W. W., A. M. V. deCarvalho, A. M. Amorim, J. Garrison, and A. R. Arbealez. 1998. Plant endemism in two forests in southern Bahia, Brazil. *Biodiversity and Conservation* 7:311–22.

Timm, R. M., and R. D. Price. 1994. Revision of the chewing louse genus *Eutrichophilus* (Phthiraptera: Trichodectidae) from the New World porcupines (Rodentia: Erethizontidae). *Fieldiana* 76:1–36.

Trucchi, E., and V. Sbordoni. 2009. Unveiling an ancient biological invasion: Molecular analysis of an old European alien, the crested porcupine (*Hystrix cristata*). *BMC Evolutionary Biology* 9:109–19.

Tuljapurkar, S. D., C. O. Puleston, and M. D. Gurven 2007. Why men matter: Mating patterns drive evolution of human lifespan. *PLoS ONE* 2(8):e785 (online).

Van Aarde, R. J. 1987. Demography of a Cape porcupine (*Hystrix africaeaustralis*) population. *Journal of Zoology* (London) 213:205–12.

Van de Wetering, J. 1980. *Hugh Pine*. Houghton Mifflin, Boston.

Van Jaarsveld, A. S. 1983. Aspects of the digestion in the Cape porcupine. *South African Journal of Animal Science* 13:31–33.

Vilela, R. V., T. Machado, K. Ventura, V. Fagundes, M. J. de J. Silva, and Y. Yonenaga-Yassuda. 2009. The taxonomic status of the endangered thin-spined porcupine, *Chaetomys subspinosus* (Olfers, 1818), based on molecular and karyological data. *BMC Evolutionary Biology* 9:29, www.biomedcentral.com/1471–2148/9/29.

Voss, R. S. 2011. Revisionary notes on neotropical porcupines (Rodentia: Erethizontidae), 3: An annotated checklist of the species of *Coendou* Lacépède, 1799. *American Museum Novitates* 3720:1–36.

Voss, R. S., and R. Angermann. 1997. Revisionary notes on neotropical porcupines (Rodentia: Erethizontidae), 1: Type material described by Olfers (1818) and Kuhl (1820) to the Berlin Zoological Museum. *American Museum Novitates* 3214:1–42.

Voss, R. S., and M. N. F. da Silva. 2001. Revisionary notes on Neotropical porcupines, 2: A review of the *Coendou vestitus* group with descriptions of two new species from Amazonia. *American Museum Novitates* 3351:1–36.

Voss, R. S., and L. H. Emmons. 1996. Mammalian diversity in neotropical lowland rainforests: A preliminary assessment. *Bulletin of the American Museum of Natural History* 230:1–115.

Wahlert, J. H. 1968. Variability of rodent incisor enamel as viewed in thin section, and the microstructure of enamel in fossil and recent rodent groups. *Breviora: Museum of Comparative Zoology* 309:1–18.

Walker, L. J. 1959. *Legends of Green Sky Hill*. W. B. Eerdmans, Grand Rapids, MI.

Werneck, F. L. 1936. Contribuição ao conhecimento dos Mallophagos encontrados nos mammiferos sul-americanos. *Memórias do Instituto Oswaldo Cruz* [online] 31(3):391–589.

Whitten, W. K. 1956. Modification of the estrous cycle of the mouse by external stimuli associated with the male. *Journal of Endocrinology* 13:399–404.

Wilby, A., M. Shachak, and B. Boeken. 2001. Integration of ecosystem engineering and trophic effects of herbivores. *Oikos* 92:436–44.

Wilson, D. E., and D. M. Reeder. 2005. *Mammal Species of the World*. 3rd ed. Johns Hopkins University Press, Baltimore.

Woods, C. A. 1973. *Erethizon dorsatum*. *Mammalian Species* 29:1–6.

Xavier, F., G. K. Joseph, B. Michael, and K. Bijula. 2000. A coprological survey of parasites of seven mammal groups at Silent Valley National Park, Kerala. *Zoos' Print Journal* 15(6):279–80.

Ziegltrum, G. J. 2008. Impacts of the black bear supplemental feeding program on the ecology in western Washington. *Human-Wildlife Conflicts* 2(2):10–16.

Zortea, M., and B. F. A. de Brito 2010. Diurnal roosts and minimum home range defined by sleeping sites of a thin-spined porcupine, *Chaetomys subspinosus* (Rodentia: Erethizontidae). *Zoologia* 27(2):209–12.

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A New World porcupine: juvenile Paraguayan dwarf porcupine, *Coendou spinosus*. The animal is in its typical habitat—up a tree. The reddish-yellow pelage (coat) is typical of juveniles and hides most body quills. Photo by Thomaz Chausson.

An Old World porcupine family: crested porcupines, *Hystrix cristata*, from Tanzania. These porcupines live in monogamous pairs and defend their young. Photo by David Bygott.

A porcupine skull, showing the teeth. The orange-stained incisors are ever-growing and curve back deep into the jaws. A powerful chewing muscle passes through the opening in front of the orbit, enhancing the action of both the incisors and the cheek teeth behind them.

Not a porcupine: an echidna. This short-beaked echidna, *Tachyglossus aculeatus*, is a monotreme. Its mouth, located at the tip of its snout, is just big enough to project the long, sticky tongue it uses to lap up ants and termites. Photo by Firo002/flagstaffotos.

Not a porcupine: a hedgehog. This West European hedgehog, *Erinaceus europaeus*, is a member of the order Erinaceomorpha, related to the shrews and moles. It is shown here foraging at night for its diet of invertebrates as well as frogs, carrion, snakes, and fruit. Photo by Samuel Palmer.

The Paraguayan dwarf porcupine displays its orange quills when threatened. Photo by Eduardo Carvalho.

The thin-spined porcupine, *Chaetomys subspinosus*, once feared extinct, has been rediscovered in Brazil's Atlantic Forest but remains vulnerable. The most divergent of the New World porcupines, it is assigned to its own subfamily. Photo by Pedro Oliveira.

African brush-tailed porcupine, *Atherurus africanus*. The porcupine vibrates the tip of its tail to produce an ominous, sibilant warning sound. Bronx Zoo.

Paraguayan dwarf porcupine, *Coendou spinosus*, climbing a tree. The bristles on the underside of the upper part of the tail are in contact with tree bark and support the animal against backsliding. Similar tail bristles are found in other New World species. Note the friction pad on top side of the tail tip. Photo by Carlos Eduardo Benfica.

Worn teeth in an old North American porcupine. The teeth in the bottom row have been worn down to the maxilla (upper jawbone). The animal, estimated to be 25 to 30 years old, must have been using cheek teeth on the opposite side to chew its food; these teeth have also lost most of their grinding surface. National Museum of Natural History.

Pelage of stump-tailed porcupine, *Coendou rufescens* (museum preparation, American Museum of Natural History). The term *rufescens* refers to the reddish color of this porcupine's quills.

Paraguayan porcupine, *Coendou spinosus*, from Minas Gerais, Brazil. Coat colors in this species are quite variable; more typical wool hairs are pale yellowish-gray, tipped in brown.
Photo by Eduardo Carvalho.

Belly fur stained by lactation in a female North American porcupine. The bleaching around the nipples is permanent.

Juvenile albino North American porcupine. The long fur and guard hairs are obscuring the quills beneath the deceptively cuddly exterior. The pink eyes show lack of melanin production; eyesight in albino porcupines is typically impaired. Photo by Karen McElmurry.

Rosette area of a young porcupine. The skin of the rosette carries little underfur, allowing it to broadcast the warning odor, a process enhanced by specially modified quills.

A male North American porcupine climbing a sugar maple. The porcupine climbs slowly but securely: its hands and feet are spread widely, claws gripping crevices in the tree bark, and its tail is pressed firmly against the trunk to prevent backsliding.

Fisher in white spruce. One reason for the fisher's success as a porcupine predator is its ability to follow and attack a porcupine up in a tree. Photo by Wayne Lynch.

Fisher emerging from a den. Fishers routinely make detours to inspect porcupine dens for occupancy. In most instances, a denned porcupine can defend itself by presenting its back. Note also the large footpads that allow fishers to travel in the snow. The five toes are diagnostic of a fisher footprint. Photo by Wayne Lynch.

Crested porcupine (*Hystrix cristata*). mother and porcupette. Because of strong parental protection, the babies of crested porcupines have extremely high survival rates in the wild. Photo by Bill Hughes.

Baby Paraguayan dwarf porcupine, *Coendou spinosus*. The thick orange-reddish fur hides most quills. There are no quills on the face, which the baby presses against its mother to nurse. Photo by Thomaz Chausson.

Beech sapling totally bark-stripped by a North American porcupine. The animals are selective in their feeding choices, not only in terms of preferred tree species but also in terms of preferences for individual trees.

Orphan male North American porcupine with Diane Honer, a wildlife rehabilitator. Found abandoned by a roadside in October, the baby weighed just 1.1 pounds (500 g)—much too small to survive on its own. The baby was fed and housed during winter and released the following spring.

Pick me up! The quills are completely relaxed on this young North American porcupine; its human rehabilitator is a friend.

North American porcupine crossing a street in downtown Juneau, Alaska. This porcupine just missed being hit by a truck. Photo by Andrei Taranchenko.

Young Brazilian porcupine (*Coendou prehensilis*) at a possible salt source in a biologist's jungle camp in Bolivia. The porcupine may also have been attracted to the liquid grease in the pan. However, Brazilian porcupines regularly visit salt licks in the jungle. Photo by Louise Emmons.

Vegetation at the Santa Lucia Biological Station in the Atlantic coastal forest, southeastern Brazil, one of the sites where the thin-spined porcupine (*Chaetomys subspinosus*) has been studied. The photo is taken from a 45-foot (15-m) platform. Visible at the upper right is a liana, in the middle right an epiphytic bromeliad, and at the lower left the top of a young palm tree (*Euterpe edulis*). Photo by Adriano Chiarello.

Thin-spined porcupine, *Chaetomys subspinosus*, in its daytime resting site. The Atlantic Forest subtype shown here is called a Restinga, characterized by a low canopy interlaced with vines and lianas. Photo by Adriano Chiarello.

Offering for a North American porcupine: an apple left at the base of a large hemlock tree in which a porcupine is in residence. The porcupine's presence is revealed by abundant nip twigs on the ground and fresh urine and droppings. This red delicious apple was gone a week later.

Quillwork box by the contemporary Ojibwe artist Lorraine Besito. The artist uses classic techniques to render leaves, branches, and background, and tufted quills to depict the quill coat of the porcupine. Photo by The Snow Goose, Ltd.

Ceramic plate, Siena, Italy. This plate celebrates the Porcupine (Istrice) District, one of the 17 districts of the town. The decoration has the traditional Istrice colors of red, blue, black, and white. Above the porcupine in the center are two flowers and a crown. Photo by Nancy Bareis.

Quill-veneer jewelry box, Ceylon, ca. 1880, featuring tropical woods with porcupine quill inlay and ivory-dot decoration. The quills are from the Indian crested porcupine, *Hystrix indica*. Gift of Dr. Elizabeth Horner to author. Photo by Nancy Bareis.

North American porcupine climbing out of an Igloo cooler following the attachment of a radio collar. The porcupine is captured by closing the Igloo top over the animal.